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Groundfish Exploitation Rates Based on Life History Parameters

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The problem considered is how to choose a fixed exploitation rate that will provide a high yield at low risk, when the investigator has no knowledge of the yield curve or the spawner–recruit relationship of the stock. Commonly employed expedients are $F_{0.1}$ and $F = M$, but these have little empirical or theoretical support. Calculations made with a range of life history parameter values typical of demersal fish and a range of realistic spawner-recruit relationships show that yield will be at least 75% of maximum sustainable yield so long as the spawning biomass is maintained in the range of about 20–60% of the unfished level, regardless of the form of the spawner–recruit relationship. A relative spawning biomass in this range can be achieved by choosing a fishing mortality rate that will reduce the spawning biomass *per recruit* to about 35% of the unfished level. This is the level of fishing mortality that maximizes the minimum yield among all of the spawner–recruit relationships considered ("maximin yield" rate, F_{mmy}). The actual value so calculated depends on the relative timing of growth, maturity, and recruitment to the fishery. In practice, F_{mmy} appears to be very close to $F_{0.1}$ except where recruitment and maturity schedules do not coincide.

Cet article traite du choix d'un taux d'exploitation fixe permettant d'obtenir un rendement élevé tout en minimisant les risques quand on ne connaît pas la courbe de rendement ou la relation reproducteurs–recrues du stock. On utilise souvent les valeurs $F_{0.1}$ et $F = M$, mais les fondements théoriques et empiriques de ces solutions sont faibles. Des calculs fondés sur différentes valeurs typiques des paramètres du cycle vital des poissons de fond et sur différentes relations reproducteurs–recrues réalistes montrent que le rendement sera d'au moins 75% du rendement maximal soutenu dans la mesure où la biomasse des reproducteurs est maintenue entre 20 et 60% de celle qui existerait si le stock n'était pas exploité et ce, quelle que soit le type de relation reproducteurs–recrues. On peut obtenir une biomasse relative de reproducteurs de cet ordre en choisissant un taux de mortalité due à la pêche réduisant la biomasse de reproducteurs par recrue à environ 35% de celle existant en l'absence d'exploitation. Parmi toutes les relations reproducteurs–recrues considérées, un tel taux de mortalité due à la pêche est celui qui maximise le rendement minimum (taux de «rendement maximin», F_{mmy}). La valeur réelle ainsi calculée est fonction des relations temporelles entre la croissance, le moment de l'arrivée à maturité et le recrutement de la pêche. En pratique, la valeur de F_{mmy} est très près de celle de $F_{0.1}$, sauf quand le recrutement et l'arrivée à maturité ne coïncide pas.

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Recommending a groundfish catch quota, or a biological upper limit for one, often consists of two steps: (i) estimating the present stock size and (ii) applying an appropriate rate of exploitation to the estimate, usually meaning a rate that will provide a high average yield in the long term without running the risk of overfishing the stock. Where the management objective is to maximize physical yield, the best approach is to apply the F_{MSY} rate of fishing mortality, defined here as the constant rate that produces the maximum average yield in the long term. Fishing at F_{MSY} will provide a yield close to the maximum obtainable by any strategy (Getz et al. 1987; Hall et al. 1988) and at the same time guarantee that on average the catches will be less than the potential yield whenever the stock happens to fall below the maximum sustainable yield (MSY) level of biomass, so that the stock will automatically rebuild from any mishap, whether it be a run of poor year-classes or some inadvertent overharvest.

During the last few decades, major advances have been made in methods of estimating stock size, but little progress has been made on the problem of estimating F_{MSY}, or any other kind of optimal exploitation rate. The difficulty, of course, is that to determine an optimal rate of exploitation, one needs to know about the density-dependent behavior of the stock in question, and that knowledge has proved elusive. It appears that for most marine fish, density dependence operates through the spawner–recruit relationship, but spawner–recruit data are typically so few or so variable that it is impossible to estimate the form of the relationship objectively with any confidence (Shepherd 1982; Sissenwine and Shepherd 1987).

Lacking any information on the yield curve (i.e. total yield as a function of fishing mortality) or, equivalently, the spawner–recruit relationship, assessment scientists have usually not been able to determine F_{MSY} and have often resorted to recommendations based on fishing mortality rates calculated from life history parameters, the most common ones being as follows:

F_{MAX}: This is the rate that maximizes yield per recruit without regard to whether sufficient spawning biomass is conserved to maintain recruitment in the future. Deriso (1982) argued that in most cases, F_{MAX} is an upper bound for F_{MSY}, but as his examples showed, it is not a sharp bound. Moreover, the F_{MAX} rate of fishing mortality is typically very high, so there is little doubt that it exceeds F_{MSY} by a wide margin and fishing at this rate for any period of time will in fact deplete

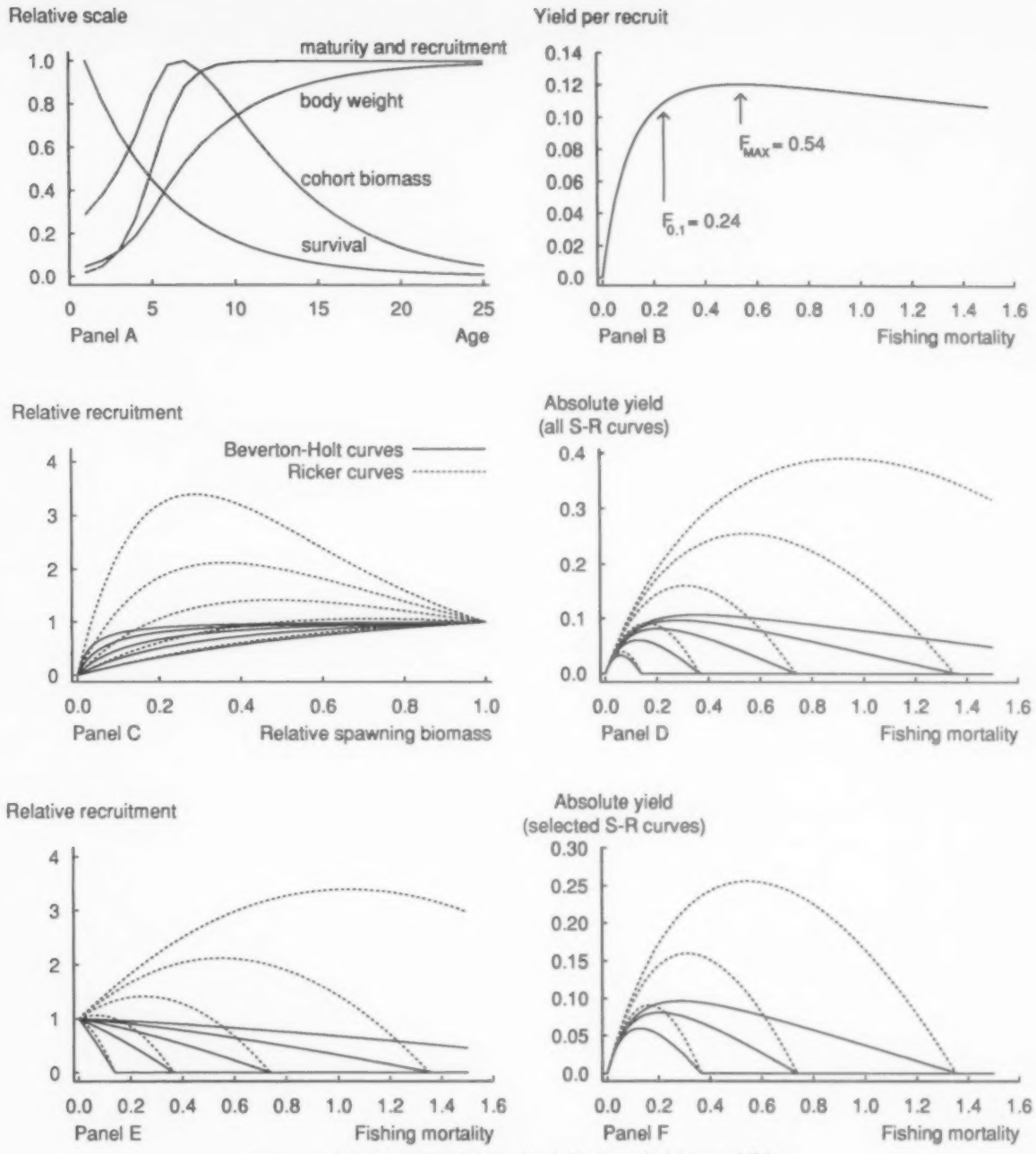

FIG. 1. Life history, recruitment, and yield of a typical demersal fish.

the spawning stock and reduce future recruitment, in some cases drastically. For these reasons, F_{MAX} has mostly passed out of favor (Deriso 1987; Sissenwine and Shepherd 1987).

$F_{0.1}$ (Gulland and Boerema 1973; Deriso 1987): This is the rate at which the slope of the yield per recruit curve (yield per recruit as a function of fishing mortality) falls to 10% of its value at the origin. Since the yield per recruit curve is typically rather flat over a wide range of higher fishing mortality rates, the $F_{0.1}$ rate usually provides something close to the maximum yield per recruit, and it is invariably much lower than F_{MAX}, so it is not so likely to deplete the spawning stock. Nevertheless, it is akin to F_{MAX} in that its calculation takes no account of its effect on the spawning stock or subsequent recruitment. Deriso (1987) discussed ways of checking on whether $F_{0.1}$ (as defined there) is sustainable and conditions under which it is equal to F_{MSY}, but in any given application it cannot be known whether $F_{0.1}$ will be greater or less than F_{MSY}.

TABLE 1. Life history parameters of New England groundfish stocks. The maturity and recruitment schedules show the ages at which 10 and 90% of a year-class are sexually mature or recruited to the fishery. Data from New England Fishery Management Council (1985, Part 5).

Stock	Natural mortality	Maturity schedule		Recruitment schedule	
		10%	90%	10%	90%
Georges Bank Atlantic cod (*Gadus morhua*)	0.2	1	5	2	4
Georges Bank haddock (*Melanogrammus aeglefinus*)	0.2	1	4	2	3
Pollock (*Pollachius virens*)	0.2	1	5	2	4
Georges Bank yellowtail flounder (*Limanda ferruginea*)	0.2	1	4	2	4
American plaice (*Hippoglossoides platessoides*)	0.2	2	6	3	5
Georges Bank winter flounder (*Pseudopleuronectes americanus*)	—	1	3	1	3

$F = M$ (Alverson and Pereyra 1969): This choice is based on the belief that F_{MSY} is often near the rate of natural mortality M. That may be true, but since there are few stocks for which F_{MSY} has been determined with any confidence, for the reasons stated, there is little empirical evidence to support the belief. Like F_{MAX} and $F_{0.1}$, this strategy takes no account of the effect of the chosen rate on spawning stock size and recruitment.

One method that has been suggested for assuring the maintenance of adequate spawning biomass is to fish at some fixed rate so long as spawning biomass remains above a threshold size, but to suspend the fishery anytime the spawning stock falls below the threshold (Hall et al. 1988; Quinn et al. 1990). This makes some sense, but without knowing the spawner–recruit relationship it is difficult to make a rational choice of either the fixed exploitation rate or the threshold. At worst this method simply imposes the requirement of choosing another parameter value in an essentially arbitrary fashion. And like other biomass-based exploitation strategies, this method is not really practical for stocks that are subject to large natural variations in equilibrium abundance, which now appear to represent the rule rather than the exception.

Another method of assuring an adequate level of spawning is to limit fishing mortality to a level that will maintain a certain value of spawning biomass per recruit, or equivalently, cohort egg production. In the form of size limits designed to guarantee one or more spawnings before capture, this is an old idea. It is also attractive, like a fixed exploitation rate, in that it will cause the spawning stock size to adjust automatically to changes in carrying capacity or to rebuild automatically from a run of poor year-classes.

Beddington and Cooke (1983) calculated the reduction in fishing mortality below F_{MAX} that would be necessary to keep spawning biomass per recruit above an arbitrary 20% of the unfished value. Botsford and Hobbs (1986) determined not only the fishing mortality rate but also the lower and upper age limits that would maximize yield subject to the constraint that cohort egg production be kept above a prescribed proportion, again chosen arbitrarily, of the unfished level. They also cited a number of other studies where cohort egg production was considered in choosing management measures.

Shepherd (1982) discussed the relationship between spawning biomass per recruit and the slope of the left-hand limb of the spawner-recruit curve and observed that a stock would collapse if fishing mortality reduced spawning biomass per recruit below a critical level. The same reasoning was used by Sissenwine and Shepherd (1987) and Gabriel et al. (1989) in deriving a level of fishing mortality at which a cohort will just replace itself at observed levels of recruit production per unit spawning biomass. This fishing mortality rate, denoted F_{rep}, is the one that reduces spawning biomass per recruit to the median observed in a set of spawner–recruit data. If the spawner–recruit data refer to year-classes produced by very small spawning stocks, F_{rep} will be an estimate of the maximum sustainable fishing mortality rate in the sense of Shepherd (1982). If the data refer to an unfished stock, F_{rep} will be zero. Thus, while F_{rep} is always a sustainable rate, it can be much higher or much lower than F_{MSY}, like the other rates calculated from life history parameters.

The present paper deals with the question of whether it is possible to calculate an exploitation rate from life history parameters that will provide a yield near MSY for any likely spawner–recruit (S–R) relationship. The approach is first to set some reasonable limits on the range of S–R relationships considered and then to construct the yield curves for those S–R relationships and a range of life history parameters typical of demersal marine fish. It will be shown that a suitable fishing mortality rate does exist for all of the cases considered, and it is always very close to the rate that reduces spawning biomass per recruit to 35% of the unfished level.

Methods

The performance of various exploitation strategies was investigated by constructing a model population similar to marine demersal stocks and computing the equilibrium yield corresponding to a range of S–R relationships and fishing mortality rates. A key step in the process was to exclude some S–R relationships from serious consideration on the grounds that they implied either too little or too much density–dependent change in reproductive success, in comparison with the performance of real populations that have been heavily fished or overfished. It was then possible to find a fishing mortality rate that would obtain a large proportion of MSY for any of the remaining S–R relationships. Finally, yield computations were performed with the same restricted set of S–R relationships and

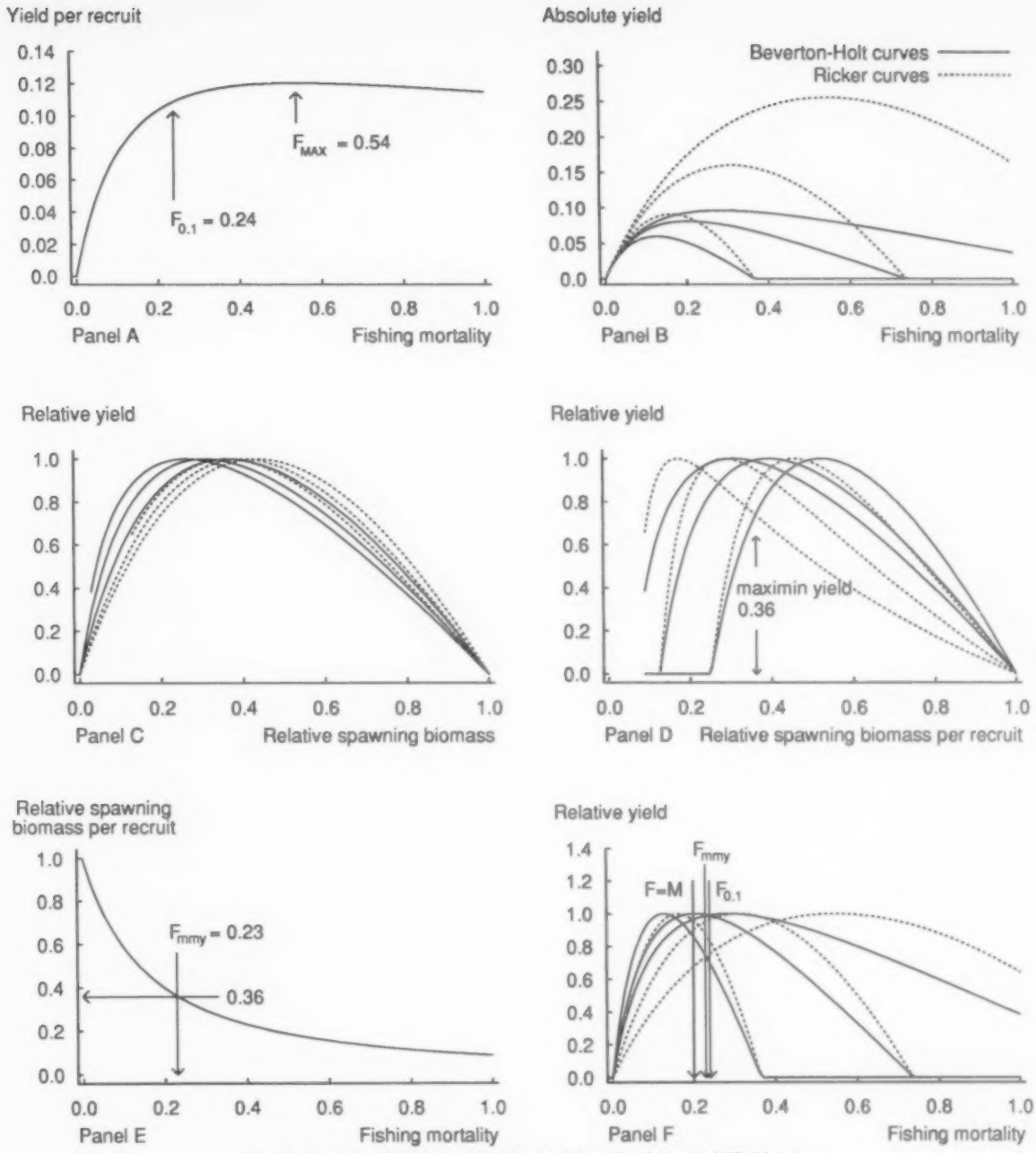

FIG. 2. Spawning biomass and yield calculations for the typical life history.

a range of life history parameter values to find a consistent method of computing the optimal fishing mortality rate from life history parameters. The steps are described below.

Life History Parameters

The central object of study for this paper was the typical demersal marine fish, which has an instantaneous natural mortality rate $M = 0.2$ and a von Bertalanffy growth (in weight) coefficient K equal to M. Schedules of recruitment to the fishery and sexual maturity were described by a logistic function that reaches 10% at age 3, 50% at age 5, and 90% at age 7. At age 5 the weight of the fish is 30% of the asymptotic weight. These standard life history features are graphed in Fig. 1A and detailed in the Appendix. As is typical, they imply a value of $F_{0.1}$ near M and a value of F_{MAX} that is much larger (Fig. 1B).

The life history parameters given above were chosen to be typical of groundfish and will be referred to as the "typical life history" below. Many stocks in the North Atlantic and North Pacific do in fact have life histories close to the typical pattern,

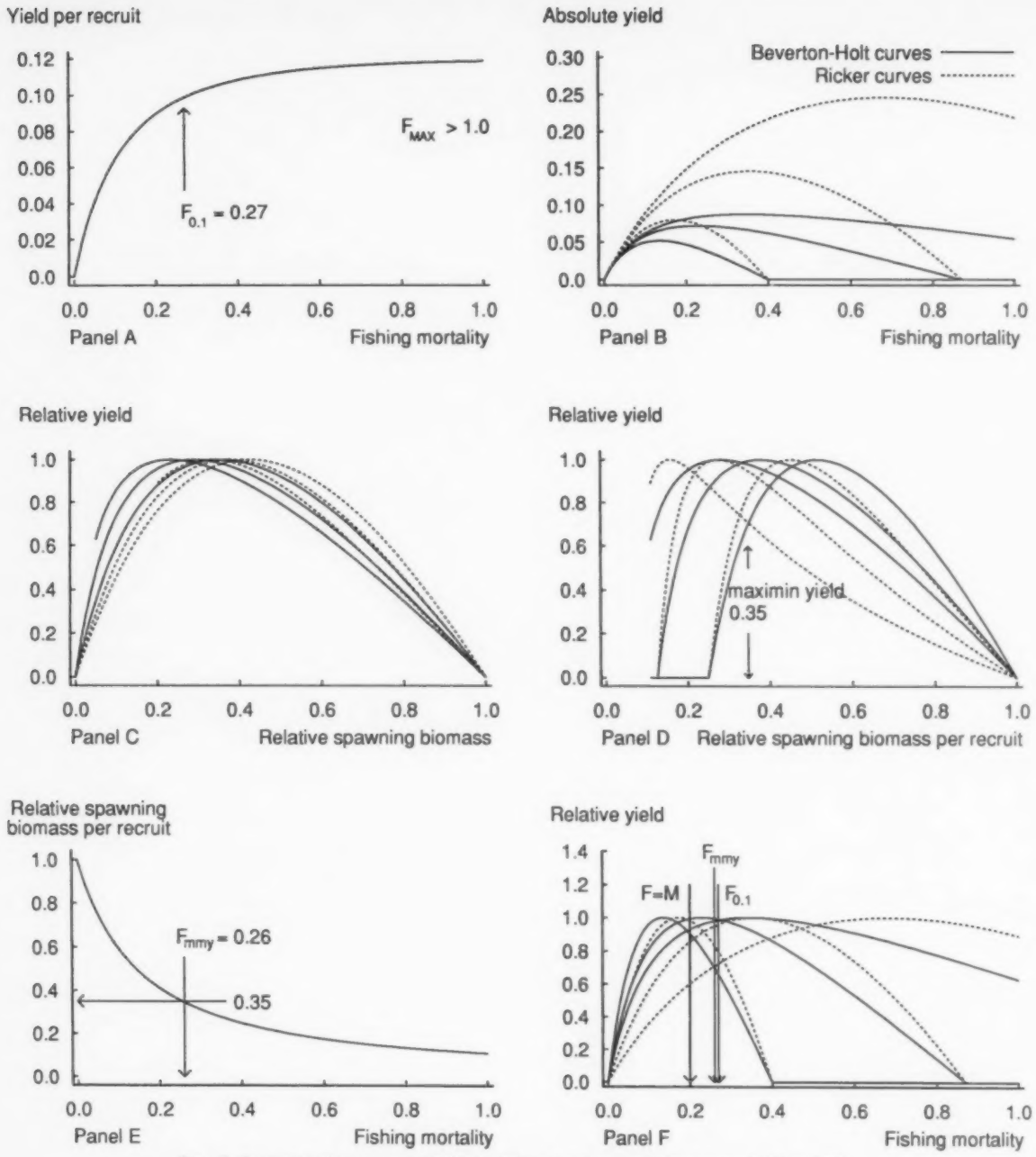

FIG. 3. Spawning biomass and yield calculations for the case of slow growth ($K = M/2$).

as exemplified by the listing of New England stocks in Table 1, but a range of natural mortality (M) and growth rates (K) occurs. Empirical data (Pauly 1980) and evolutionary theory (Roff 1984) both indicate a correlation of K and M, and they are often of similar size, but the ratio M/K is substantially less or greater than unity for many stocks. Therefore, while M and K are both set at 0.2 in the typical life history, other values (0.1 and 0.4) are used later in the paper to investigate the effect of different absolute and relative values. Similarly, while recruitment and maturity schedules often coincide, they are quite different for many stocks. These two schedules are therefore taken to be coincident for the typical life history, but a shift of one relative to the other is considered later in the paper. The duration of the recruitment and maturity schedules, e.g. the 4 yr from 10% maturity to 90% maturity in the typical life history, does vary among stocks, but different values are not considered in this paper because the effect of schedule duration on yield comparisons is minor.

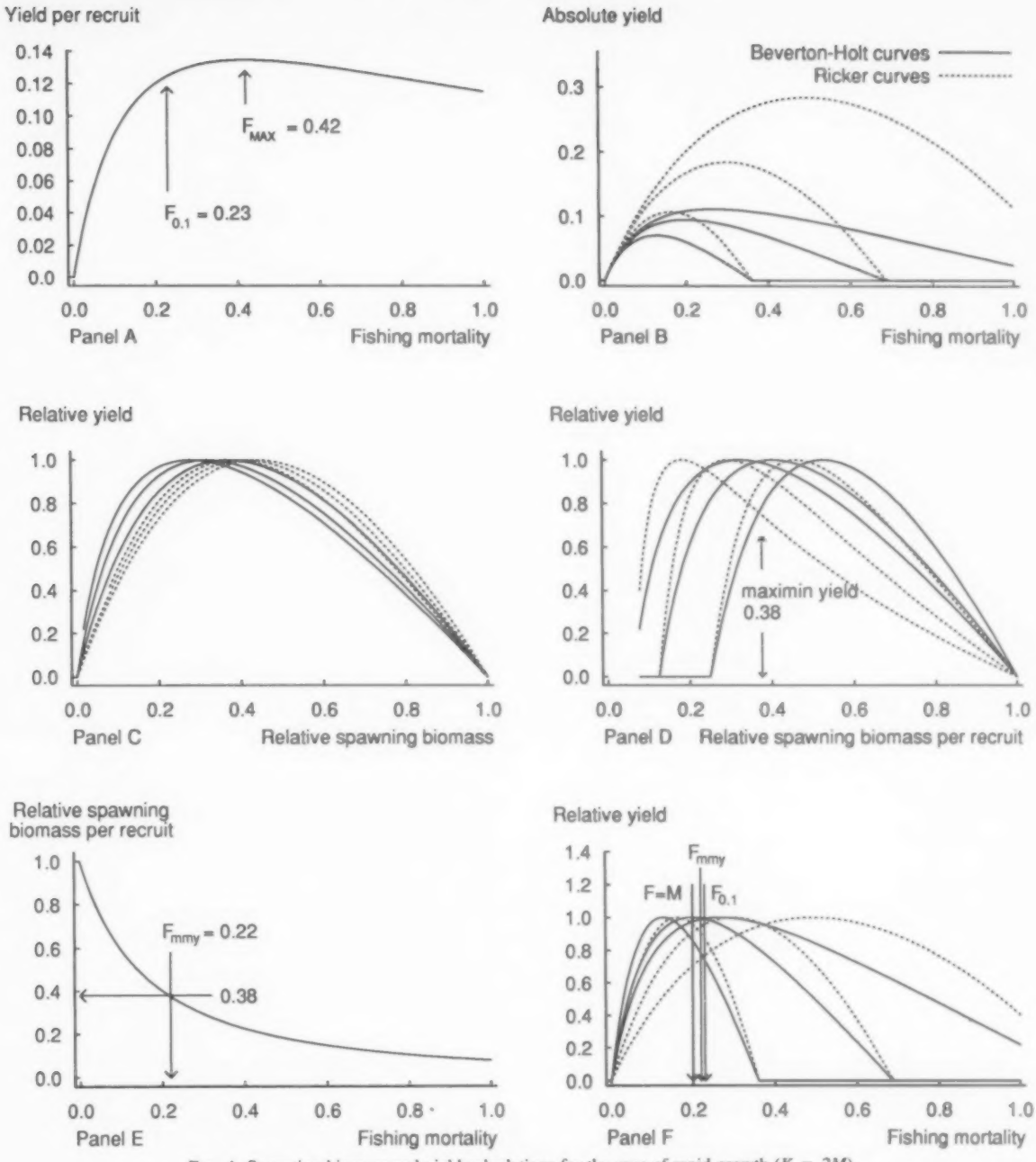

FIG. 4. Spawning biomass and yield calculations for the case of rapid growth ($K = 2M$).

Initial Specification of Spawner-Recruit Relationships

The S–R relationships considered initially were sets of the Beverton–Holt and Ricker forms, representing asymptotic and domed curves (Fig. 1C). A large number of other forms might be considered, but these two can approximate the other forms adequately.

The formulation of the relationships is that of Kimura (1988): each curve describes *relative* recruitment as a function of *relative* spawning biomass (both measured relative to their unfished levels) and is determined by a single shape parameter. The value of the shape parameter determines the potential for density–dependent increase in the specific reproductive rate, meaning number of recruits per unit spawning biomass. The five initial curves of each form represent potential increases in specific reproductive rate by factors of 2, 4, 8, 16, and 32, meaning that at very low spawning stock size, spawners are 2–32 times as successful as they are at the unfished spawning stock size, according to the shape parameter of the S–R curve. It will be argued below that this range of parameter values exceeds what can realistically be expected in nature, at both

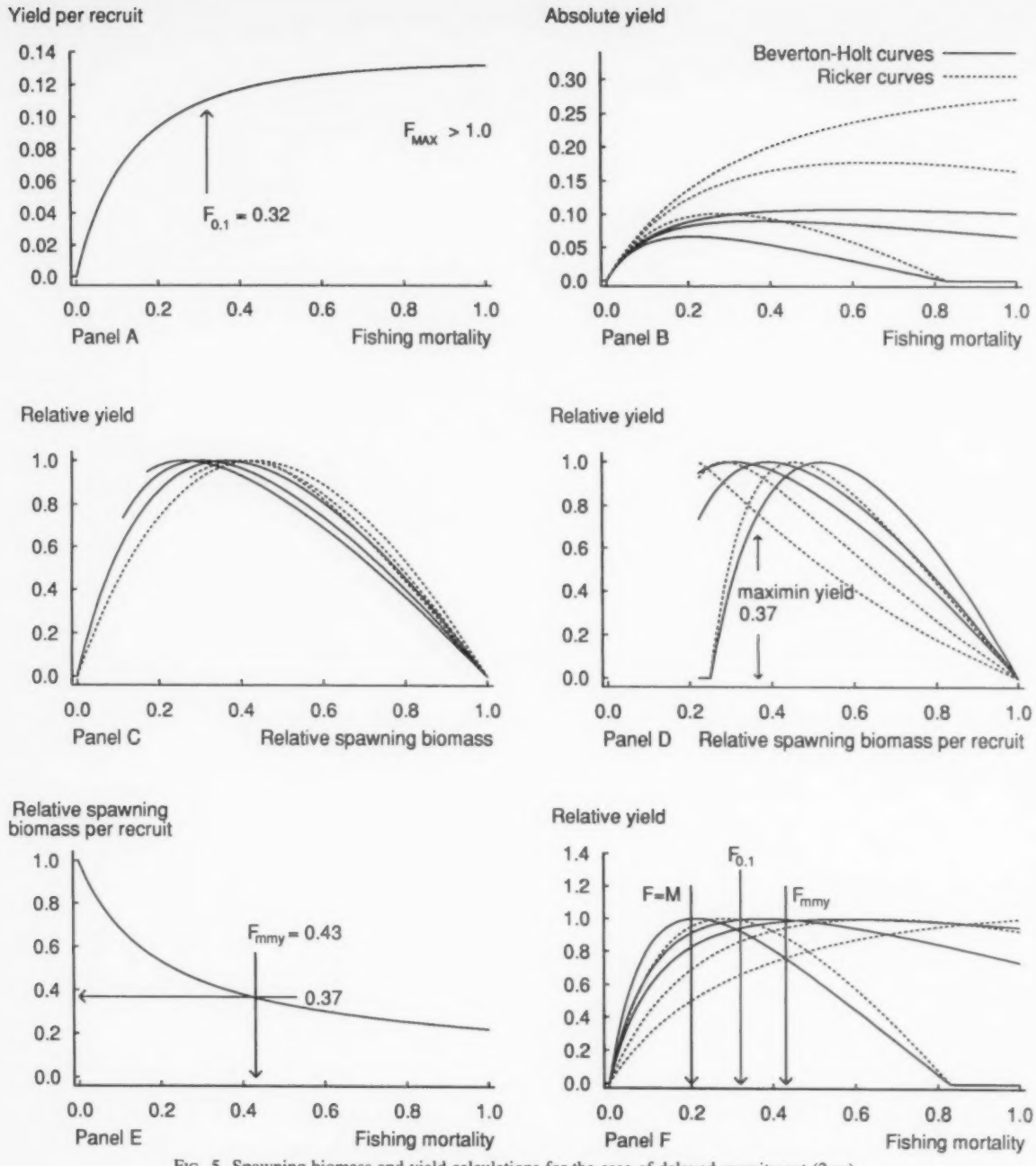

FIG. 5. Spawning biomass and yield calculations for the case of delayed recruitment (2 yr).

the upper and lower ends, so that a subset of the initial S–R relationships will serve as a reasonable approximation of the true range in nature.

Exclusion of Some Spawner–Recruit Relationships

The yield curves corresponding to the initial S–R curves are extremely diverse, with F_{MSY} values ranging from less than 0.1 to almost 1.0 (Fig. 1D). If all of the S–R curves had to be considered, there would clearly be no possibility of choosing a compromise fishing mortality rate that would serve reasonably well for all of the yield curves.

But some of the S–R relationships can be ruled out on the basis of experience and common sense. The least density-dependent pair of S–R curves implies that the stock would be driven to extinction by a fishing mortality rate less than M (Fig. 1E), and the next pair implies extinction at a fishing mortality rate less than $2M$. This could be true for some stocks, but the author is not aware of any cases. Meanwhile there are numerous examples of demersal stocks that have sustained fishing mor-

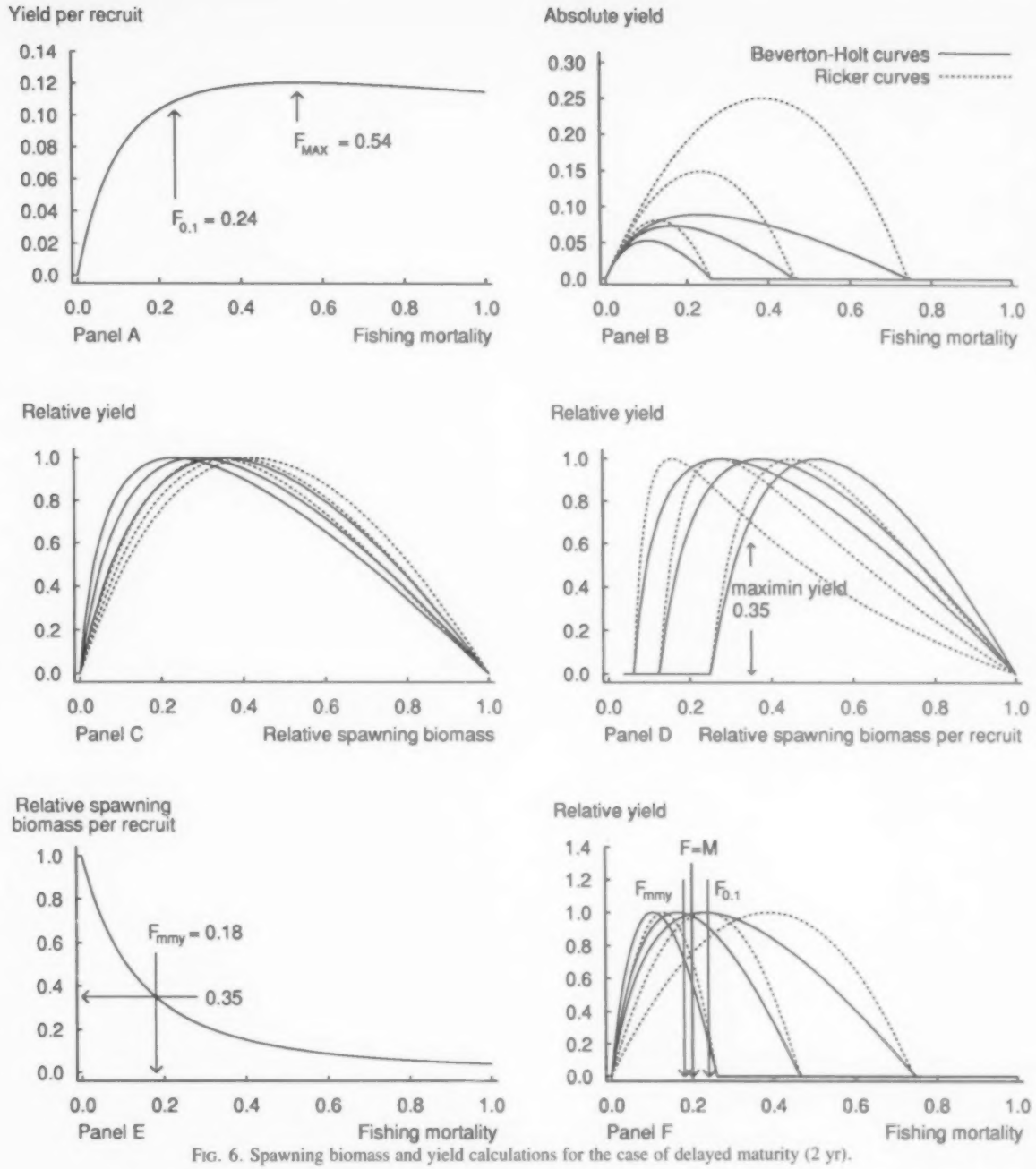

FIG. 6. Spawning biomass and yield calculations for the case of delayed maturity (2 yr).

tality rates well above $2M$ for long periods. Lacking clear evidence for a particular stock, therefore, it seems reasonable to exclude the lowest pair of S–R curves from the range to be considered and to treat the next pair as a lower bound for the S–R relationship.

At the other extreme, the most density-dependent pair of curves indicates hardly any ill effect of fishing at $F = 1.0$. Again, this may be true for some stocks, particularly where gear regulations postpone recruitment until after one or two spawnings, but in most cases, fishing at such a high rate can be expected to reduce recruitment and yield dramatically. Even the next lower pair of curves seems quite optimistic, as they imply that the stock could sustain $F = 1.3$ or so. It therefore seems reasonable to rule out the uppermost pair of S–R curves and to treat the next pair as an upper bound on the S–R relationship.

With the extreme portions of the initial range of S–R relationships excluded, it is possible to choose a fishing mortality rate in the range of 0.20–0.25 that will provide a large fraction of MSY regardless of which of the remaining S–R curves is

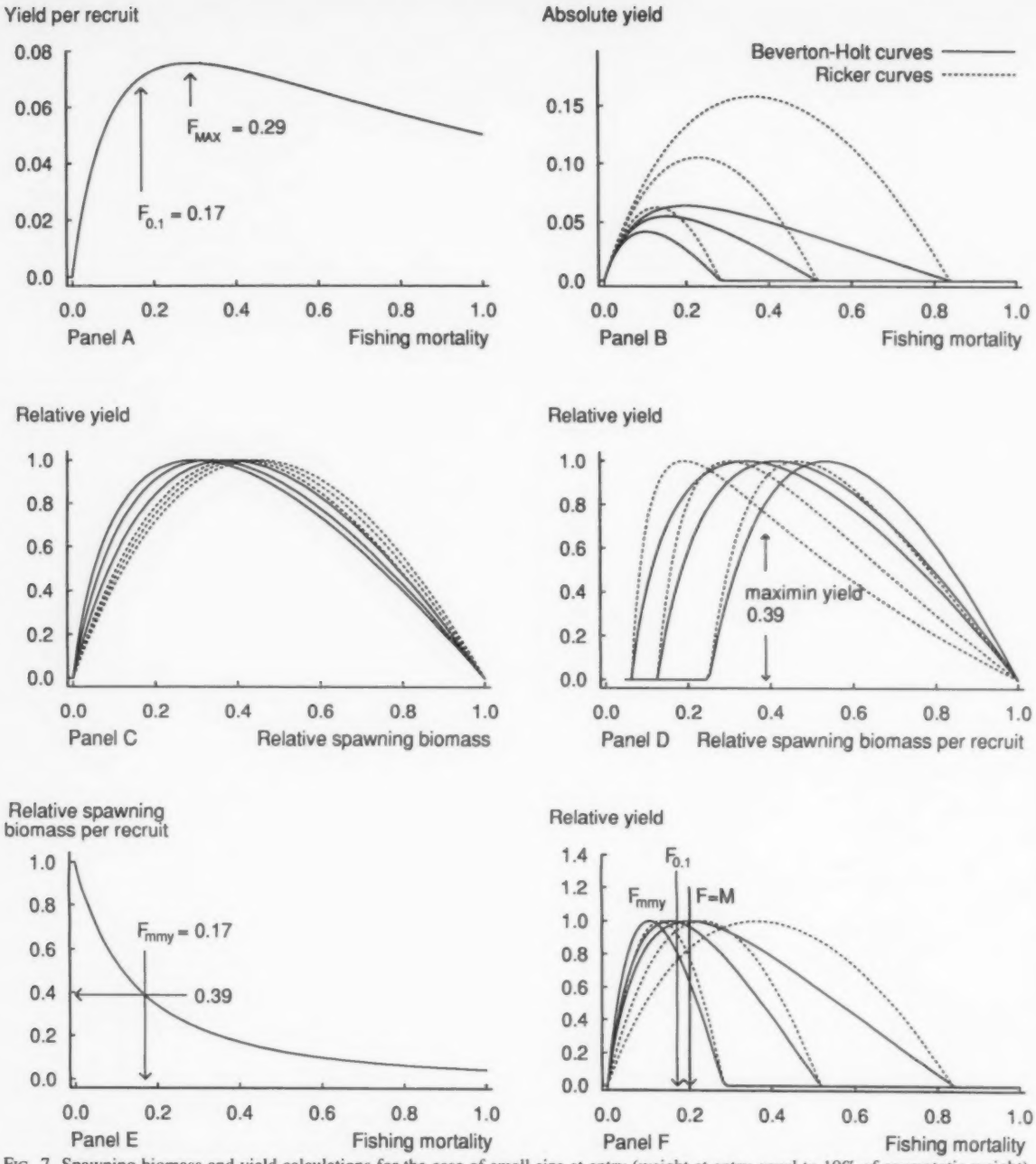

FIG. 7. Spawning biomass and yield calculations for the case of small size at entry (weight at entry equal to 10% of asymptotic weight).

correct (Fig. 1F). Specifically, $F = 0.23$ will provide about 75% of MSY if either the most density-dependent Ricker curve (corresponding to the uppermost yield curve) or the least density-dependent Beverton–Holt curve (corresponding to the lowermost yield curve) is the correct one. For any of the intermediate S–R and yield curves, $F = 0.23$ will provide a larger fraction of MSY.

This is essentially the procedure devised by Lenarz (1984) to choose a fishing mortality rate for widow rockfish (*Sebastes entomelas*): decide which S–R curves to entertain, plot the corresponding yield curves, and choose a fishing mortality rate that performs well across the entire range of possible yield curves.

Investigation of Exploitation Strategies

The Lenarz procedure is adequate by itself for choosing a fishing mortality rate in any particular case, but it was of interest to pursue the study of the case at hand further to see what features were invariant with respect to the S–R relationship,

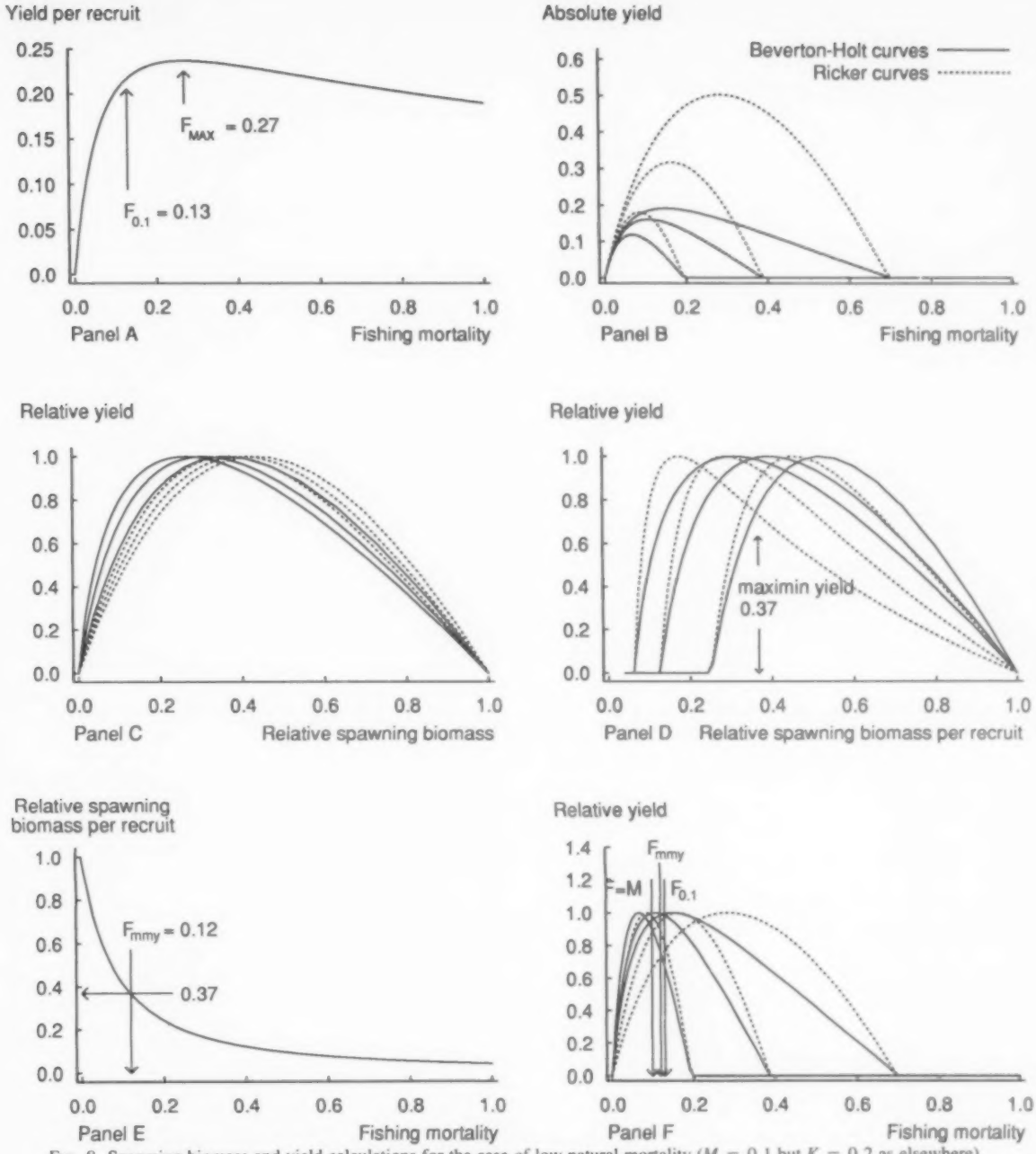

FIG. 8. Spawning biomass and yield calculations for the case of low natural mortality ($M = 0.1$ but $K = 0.2$ as elsewhere).

and in particular whether a suitable fishing mortality rate could be calculated from the life history parameters alone. The results presented below were obtained by investigating the behavior of the model population.

Results

Relationship between Spawning Biomass and Yield

Even with the extreme S–R relationships excluded, the plot of yield against fishing mortality depends quite strongly on the form of the S–R curve (Fig. 2B, same as 1F). But when relative yield (i.e. yield as a fraction of MSY for each yield curve) is plotted against relative spawning biomass, all of the curves nearly coincide (Fig. 2C). This result holds even when the extreme S–R curves are included, and it holds for a wide variety of life history parameters, including all combinations of all the parameter values listed in the Appendix. Moreover, the graph has a fairly broad summit, indicating that a yield of at least 75% of MSY would be obtained by *any* strategy that kept the

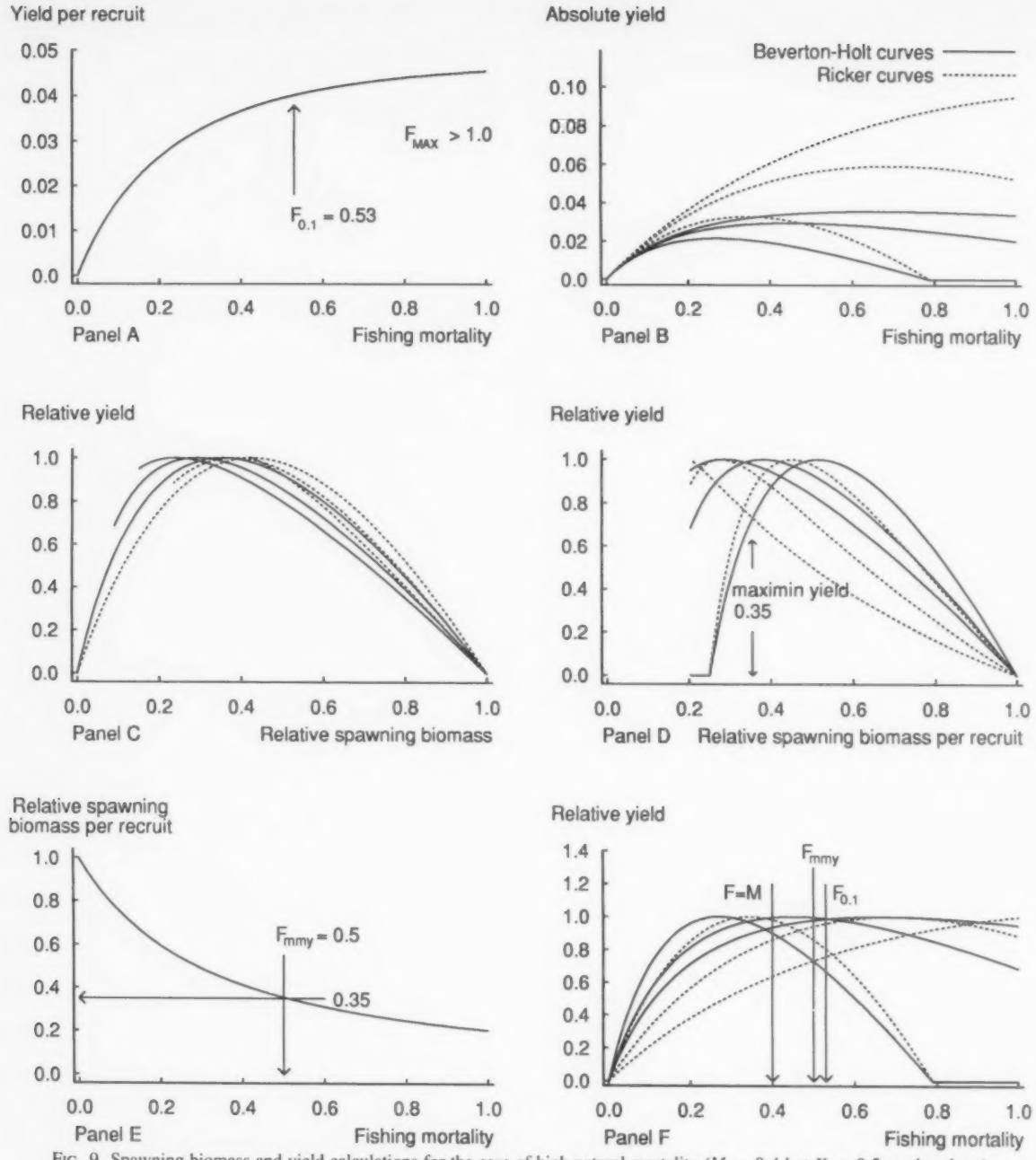

FIG. 9. Spawning biomass and yield calculations for the case of high natural mortality ($M = 0.4$ but $K = 0.2$ as elsewhere).

relative spawning biomass anywhere in the range of roughly 20–60% of the unfished level.

By itself, the very consistent relationship between relative spawning biomass and relative yield, nearly identical for all S–R curves, argues for a biomass-based strategy rather than an exploitation rate strategy. It is clear that even if unfished spawning biomass were known only very roughly, say with a precision of the half-to-double variety, one could still be reasonably sure of getting something close to MSY simply by holding the spawning biomass in the vicinity of 35–40% of the estimated unfished level.

Relationship between Spawning Biomass per Recruit and Yield

An alternative strategy that does a fairly good job of exploiting the same relationship is to lower the relative spawning biomass *per recruit* to a point somewhere near the middle of the 20–60% range (Fig. 2D). In this case the curves do not coincide as well, but there is a level of spawning biomass per recruit that provides a large fraction of MSY even under the least

TABLE 2. Life history parameters of Bering Sea walleye pollock. The recruitment schedule is from Quinn and Collie (1990); all other values from Wespestad (1989).

Age	Natural mortality	Proportion mature	Proportion recruited	Average body weight (kg)
2	0.45	0.008	0.127	0.105
3	0.30	0.289	0.438	0.251
4	0.30	0.641	1.000	0.409
5	0.30	0.842	1.000	0.465
6	0.30	0.901	1.000	0.650
7	0.30	0.947	1.000	0.798
8	0.30	0.963	1.000	0.892
9+	0.30	0.970	1.000	0.970

favorable S–R curves. This is shown as the "maximin yield" in Fig. 2D because it is the maximum of the minimum yields at each level of spawning biomass per recruit. (Alternatively, it is the maximum of the minimum yields at each rate of fishing mortality.) It occurs at 36% of the unfished value of spawning biomass per recruit, which corresponds to a fishing mortality rate of 0.23 (Fig. 2E), denoted F_{mmy}. For the typical life history, this is almost identical to $F_{0.1}$, and close to M. Any one of those rates would take a large fraction of MSY in this case (Fig. 2F). F_{mmy} takes about 75% of MSY if either of the extreme S–R curves applies and 90% or more of MSY if one of the intermediate S–R curves applies.

Effect of Altering Life History Parameters

Figures 3–7 depict the same sorts of calculations and comparisons for life histories with one parameter changed in each case to show the effects of slower and faster growth (relative to M), delayed recruitment to the fishery (i.e. 50% recruitment shifted to age 7 while 50% maturity remains at age 5), delayed maturity (the reverse), and small size at entry (50% recruitment occurring at 10% of asymptotic weight rather than 30% of asymptotic weight). In all cases the relationship of relative yield to relative spawning biomass is very close for all S–R curves, and the "maximin yield" fishing mortality rate F_{mmy} occurs at a level of spawning biomass per recruit close to 35% of the unfished level. The same results are obtained when parameter values are varied simultaneously rather than singly.

In all but two of the cases shown, F_{mmy} is nearly indistinguishable from $F_{0.1}$, and those cases are instructive. When recruitment is delayed (Fig. 5), so that fish have a chance to spawn before sustaining any fishing mortality, F_{mmy} is much higher than both $F_{0.1}$ and M, as it should be to achieve the proper reduction in relative spawning biomass. When maturity is delayed (Fig. 6), so that fish sustain some mortality before spawning, F_{mmy} is considerably lower, in this case to prevent an excessive reduction in spawning biomass. These examples show that $F_{0.1}$ is probably a reasonable exploitation rate so long as the recruitment and maturity schedules of a stock coincide, but that F_{mmy} is generally preferable because it can be relied on to maintain an appropriate level of spawning biomass per recruit for any set of recruitment and maturity schedules.

Effect of Error in the Estimate of Natural Mortality

In most cases, F_{mmy} is also close to the natural mortality rate M, and its value is of course quite sensitive to the value of M, which is notoriously difficult to estimate. In many groundfish assessments, the estimate $M = 0.2$ is used more out of habit than conviction. For the typical life history (Fig. 2), F_{mmy} is 0.23 when M is taken to be 0.2. If the true value of M were 0.1, but all other parameters were the same, the desired value of F_{mmy} would be 0.12 and fishing at $F = 0.23$ could severely deplete the stock (Fig. 8). Similarly, if the true value of M were 0.4 and all other parameters were the same, the desired value of F_{mmy} would be 0.50 and fishing at $F = 0.23$ might obtain only about half of MSY (Fig. 9).

Discussion

Consideration of Alternative Strategies

The results presented above suggest two methods for obtaining a high yield with little risk when one has no knowledge of the S–R relationship. The first is to hold spawning biomass at 20–60% of the unfished level and harvest the surplus production, whatever that turns out to be. The second is to fish consistently at $F = F_{mmy}$, whatever happens to stock biomass.

The first strategy, presumably implemented with some kind of smoothing procedure to stabilize annual catches, is clearly preferable when a stock's equilibrium abundance (i.e. environmental carrying capacity) appears to be fairly constant and it is possible to estimate the unfished spawning stock biomass with reasonable confidence. Great precision is not required. The difficulty in many cases is that equilibrium abundance varies considerably in the medium term, so that one can never be sure what the unfished level might be, or where it might be headed. In the Alaska region, for example, the majority of groundfish stocks (particularly cod and several species of flatfish) have exhibited 5- to 10-fold changes in abundance during the last 20 yr while being fished at very low exploitation rates or not at all (North Pacific Fishery Management Council 1989a, 1989b). In these cases it is clearly not practical or rational to attempt to maintain a certain spawning biomass level.

For such highly variable stocks, the F_{mmy} strategy or something similar may be the best approach, since it will allow the fishery to track the yield curve through large natural changes in equilibrium abundance, extracting something near MSY under any regime. The main drawback to this strategy is that it is less robust that the biomass strategy. As the results show, the F_{mmy} strategy is more sensitive to the form of the S–R relationship than is the biomass strategy. It is also more sensitive to errors that can enter its calculation. A 50% error in the estimate of M can produce a target F_{mmy} that will perform quite poorly, while a 50% error in the estimate of unfished spawning biomass will produce a target spawning biomass that will perform quite well (i.e. provide a large fraction of MSY).

Hybrid strategies could be developed for cases where a catch limit recommendation could be made either way but with less than complete confidence. A hybrid strategy could take on some of the adaptive behavior of an exploitation rate strategy while preserving some of the robustness of a biomass strategy.

Examples: Bering Sea Pollock and Cod

The walleye pollock (*Theragra chalcogramma*) stock of the eastern Bering Sea is unusual among Alaska groundfish stocks in that its abundance has varied by a factor of only three or so over the last two decades. Fishing mortality rates have been moderate (mostly much less than $M = 0.3$). There is no indication that carrying capacity has changed greatly, and

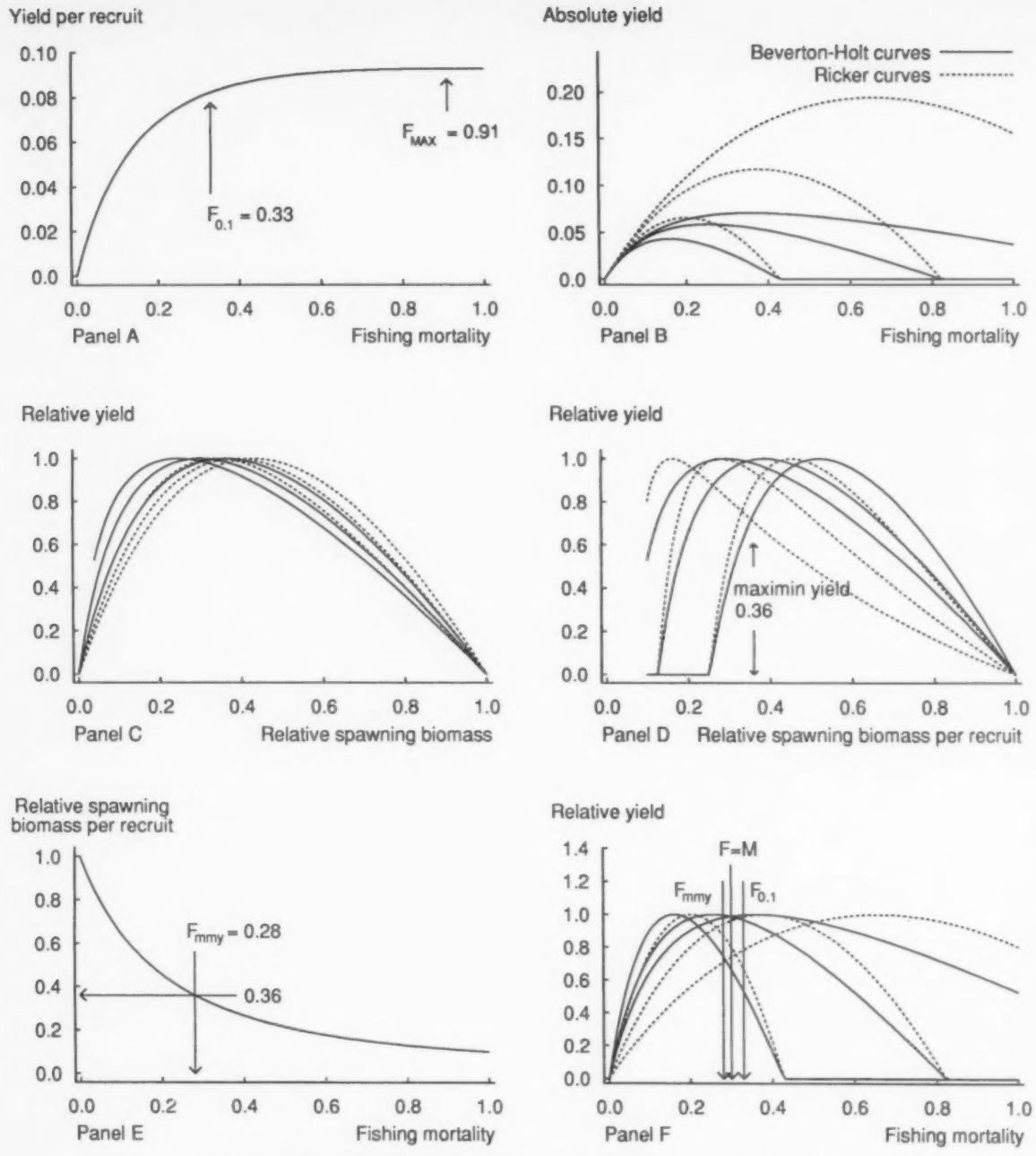

FIG. 10. Spawning biomass and yield calculations for Bering Sea walleye pollock.

recruitment (age 2) has averaged about 10 billion fish, with considerable year-to-year variation but no trend. S–R data suggest a domed S–R relationship, but the points are so scattered that the form of the relationship is uncertain. Stock histories and assessments are given in Wespestad (1989) and Quinn and Collie (1990).

This stock is clearly a candidate for a biomass-based strategy. The unfished spawning stock size can be estimated from the recent recruitment level and the unfished spawning biomass per recruit, calculated from life history parameters (Table 2). It is about 10 million metric tons. (If the S–R relationship is in fact dome-shaped, this estimate will be too high, since the recent recruitment level will be somewhat greater than the unfished level, but for present purposes the possible error is not important.) A target spawning biomass of 4 million metric tons, at the center of an acceptable range of 2–6 million metric tons, will provide the bulk of MSY regardless of the actual form of the S–R relationship. Production modelling by Quinn and Collie (1990) indicated that the MSY level of *exploitable* biomass is about 6 million metric tons, which corresponds to a spawning

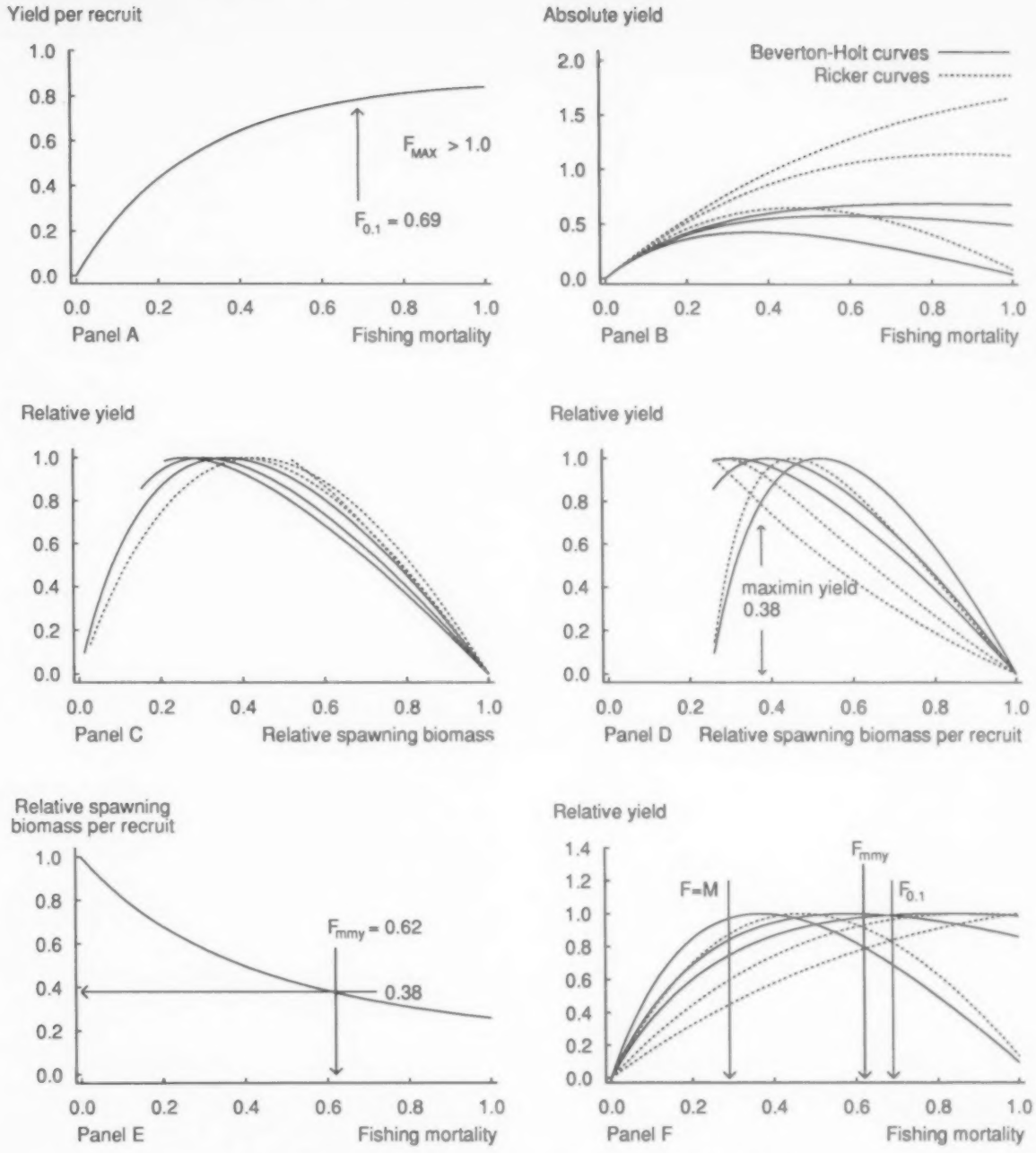

FIG. 11. Spawning biomass and yield calculations for Bering Sea Pacific cod.

stock biomass of 4.5–5.0 million metric tons.

Alternatively, the stock could be fished at a steady F_{mmy} = 0.28 (Fig. 10), which happens to be very close to Quinn and Collie's (1990) estimate of F_{MSY} = 0.32.

Either way, the exploitation strategies developed in this paper, which require only life history parameters, agree very well with the strategies based on a long series of empirical data on the productivity of the pollock stock. This provides some reassurance for adopting one or the other strategy in cases where empirical productivity data are unavailable or unreliable, such as Bering Sea Pacific cod (*Gadus macrocephalus*).

The Pacific cod stock of the Bering Sea has increased by roughly an order of magnitude since the mid-1970's. Fishing mortality rates have been low or nil during most of this period. Carrying capacity may have changed dramatically, or the upsurge in stock abundance may be the chance result of a few

TABLE 3. Life history parameters of Bering Sea Pacific cod (Dr. G. G. Thompson, National Marine Fisheries Service, Seattle, WA, pers. comm.).

Age	Natural mortality	Proportion mature	Proportion recruited	Average body weight (kg)
3	0.29	0.004	0.036	0.651
4	0.29	0.114	0.086	1.726
5	0.29	0.666	0.208	3.149
6	0.29	0.946	0.498	4.721
7	0.29	0.990	0.982	6.289
8+	0.29	0.997	0.397	7.752

strong year-classes. Fish of this stock are difficult to age, so catch at age has been estimated from catch at length, with the result that data on year-class strength are imprecise. In this situation, fitting a production model or S–R relationship is a difficult proposition. Thompson (1989a) reviewed the stock history and discussed alternative management strategies.

This stock is clearly a candidate for a fixed exploitation rate strategy, which will perform reasonably well through large fluctuations in equilibrium abundance. The life history parameters (Table 3) imply a full-recruitment $F_{mmy} = 0.62$, which is the rate required to reduce spawning biomass per recruit to the maximin yield level of 38% (Fig. 11). F_{mmy} is high in this case because growth is rapid, recruitment lags maturity, and only one age-class (age 7) is more than 50% vulnerable to the fishery. This example illustrates the importance and utility of determining the effect of a given fishing pattern on spawning biomass per recruit, not only to avoid overfishing but also to avoid underfishing.

Hazards and Limitations

The approach to choosing an exploitation rate developed here is based on the Lenarz procedure of computing a separate yield curve for each of several S–R relationships. An alternative procedure would be to set a probability distribution on the collection, or on the shape parameter, and compute a single expected yield curve. There are several pitfalls here. By not inspecting the yield curve corresponding to each S–R curve, one may include some clearly unrealistic S–R relationships in the calculations. Also, one may choose an optimum F that carries the risk of severely depleting the stock under one or more of the plausible S–R curves, when the aim is to maximize expected yield subject to the constraint that there be no serious risk of overfishing, as is often the case.

Perhaps the worst hazard is that a single expected yield curve, once computed, would be treated as an estimate of the actual yield curve of the stock, which it most certainly would not be. It should be stressed that the methods presented above supply only one result, namely a relative spawning biomass level or a fishing mortality rate that will obtain a large fraction of MSY. None of the calculations supplies any information about the actual magnitude of MSY, or the value of F_{MSY}, or the consequences of fishing at rates above F_{mmy}.

Physical Yield and Economic Yield

Finally, it should be kept in mind that the exploitation strategies derived here only serve to obtain a physical yield near the maximum. As shown by Thompson (1989b), this sort of strategy can be, and usually is, far from any rational economic strategy. It may be useful in cases where the management objective happens to be a high physical yield, but in other cases its main function will be simply to provide a biological reference point or upper limit for quota deliberations. On the other hand, there is no reason why the methods used above could not be applied to the problem of locating an exploitation strategy that would reliably obtain something close to the maximum of some chosen economic value, much as Die et al. (1988) employed standard per-recruit calculations to investigate the utility rather than the physical yield that would be obtained from different management measures.

Acknowledgments

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Appendix. Mathematical Details

Yield computations were performed with a range of life history parameters (natural mortality, growth, recruitment, and maturity schedules) centered on the values typical of groundfish stocks, and a range of spawner–recruit (S–R) relationships. Life history parameters were treated as fixed and independent of stock size. The parameter values and computations are detailed below.

Natural Mortality

For the typical life history, the instantaneous rate of natural mortality was $M = 0.2$/yr. Other values used in some of the computations were 0.1 and 0.4/yr.

Standard Age at Entry

The standard age at 50% maturity and 50% recruitment was $k = 5$ yr. This value was chosen because groundfish tend to mature and recruit at an age around $1/M$ and the standard M was 0.2, but the actual value of k employed in the calculations is unimportant. Exactly the same results would have been obtained with any other value of k.

Growth

Growth in weight was represented by a Brody curve, usually with coefficient $\rho = \exp(-M)$. This is the same thing as a von Bertalanffy curve with $K = M$. Let

w_a = weight (mean weight in catch) at age a
w_k = weight at the standard age at entry k
w_∞ = asymptotic weight
$c = w_k/w_\infty$
ρ = Brody growth coefficient.

For ages $\geq k$, the growth equation was

$$w_{k+i} = w_\infty(1 - \rho^i) + \rho^i w_k$$
$$= w_\infty[1 - \rho^i(1 - c)].$$

This is equivalent to equation 1.16 of Schnute (1985). For ages $< k$, a tail was appended to the standard Brody curve that has the same slope at age k and growth increments that decrease toward age zero in the same way (but not at the same rate) that growth increments decrease beyond age k (see Fig. 1A). The equation for ages $\leq k$ was

$$w_{k-i} = w_k\eta^i \text{ where } \eta = \rho^{[(1-c)/c]}.$$

The tail was added to avoid the negative weights that can occur at ages $< k$ when the standard Brody curve is used. The weights so determined are sensible enough, but they have little effect on the calculations because the weights must be small in any case and the age groups in question are only fractionally mature and recruited.

For the typical life history, $\rho = \exp(-M) = \exp(-0.2) = 0.82$ and $c = 0.3$, the latter value chosen to make the yield-per-recruit curve typically flat-topped. Other values used in some of the computations were $\rho = \exp(-0.1)$ and $\exp(-0.4)$ and $c = 0.1$. Asymptotic weight w_∞ was simply set to unity.

Maturity and Recruitment Schedules

Let k_m = age at 50% maturity (= standard age at entry k in almost all cases). The proportion m_a mature at age a was given by the logistic

$$m_a = 1/\{1 + \exp\{-\gamma(a - k_m)\}\}$$

with slope parameter $\gamma = 1$. At this value of γ, there is a period of 4 yr between the ages at which fish reach 10% maturity and 90% maturity, which is typical. Partial recruitment to the fishery was represented by the same logistic, but with an age at 50% recruitment k_r that could be different from k_m. To investigate the effect of delayed maturity, k_m was raised to $k + 2$ with $k_r = k$ as usual. To investigate the effect of delayed recruitment, k_r (and only k_r) was raised to $k + 2$. The parameter k, used in the growth equation, was always kept at 5.

Calculation of Yield per Recruit and Spawning Biomass per Recruit

Given the growth, maturity, and recruitment schedules above, and any fishing mortality rate F, it was straightforward to compute yield per recruit and spawning biomass per recruit in the usual way.

Spawner–Recruit Curves

The customary formulation of the Ricker S–R curve is

$$R = \alpha S \exp(-\beta S).$$

Let S_o denote the equilibrium spawning biomass in the absence of fishing and R_o the corresponding unfished level of recruitment. With $A = \beta S_o$, the Ricker equation can be rewritten

$$(R/R_o) = (S/S_o)\exp[A(1 - S/S_o)]$$

so that relative recruitment (R/R_o) is given as a function of relative spawning biomass (S/S_o) and the single shape parameter A (Kimura 1988).

Another way of writing the equation is

$$(R/S) = (R_o/S_o)\exp[A(1 - S/S_o)]$$

which provides the means of solving for the equilibrium spawning biomass at any fishing mortality rate F. The ratio (R_o/S_o) is just the reciprocal of spawning biomass per recruit in the absence of any fishing, and the ratio (R/S) is the reciprocal of spawning biomass per recruit when F is applied. Once these ratios have been computed, the S–R equation can be solved for (S/S_o).

The one-parameter form of the Beverton–Holt S–R curve is

$$(R/R_o) = (S/S_o)/[1 - A(1 - S/S_o)].$$

For all of the computations in this paper, R_o was set to unity, and S_o was then determined by the values of the life history parameters. The initial values of A used for the Ricker curves were 0.693, 1.386, 2.079, 2.773, and 3.466. For the Beverton–Holt curves the values were 0.500, 0.750, 0.875, 0.938, and 0.969. For both forms of the S–R relationship, these shape parameters imply potential density-dependent increases in reproductive success (recruits per unit spawning biomass) by factors of 2, 4, 8, 16, and 32, respectively.

Calculation of Absolute and Relative Yields

Yield per recruit and spawning biomass per recruit were calculated for each value of F, as explained above. For each S–R curve and each value of F, equilibrium spawning biomass and recruitment were determined by solving the S–R equation, and absolute yield was obtained as $Y = R \cdot (Y/R)$. It was then straightforward to locate MSY for each S–R curve and finally to obtain relative yield (Y/MSY) for each F.

Whelk (*Buccinum undatum*) Movement and Its Implications for the Use of Tag–Recapture Methods for the Determination of Baited Trap Fishing Parameters

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Sainte-Marie, B. 1991. Whelk (*Buccinum undatum*) movement and its implications for the use of tag–recapture methods for the determination of baited trap fishing parameters. Can. J. Fish. Aquat. Sci. 48: 751–756.

The tag–recapture method has been used to measure the field of attraction and the effective fishing area of a baited trap. The possibly conflicting experimental conditions required for the determination of these two parameters are, respectively, that tagged animals do not move and that they behave as undisturbed animals, prior to exposure to bait odour. Field observations and in situ experiments were conducted on the north shore of the Gulf of Saint Lawrence in 1988 and 1989 to compare behaviour of undisturbed and tagged whelks (*Buccinum undatum*). In the daytime, ~75 % of undisturbed whelks were quiescent, being either buried and oriented randomly or static and oriented downstream, while the remainder moved across stream at 2–5 cm·min^{-1}. In contrast, >97 % of tagged whelks oriented in nonrandom directions and moved at equal or greater speeds, on average, 2.2–9.2 m from release points in less than 6 h. Because neither of the two basic conditions was met, tag–recapture experiments would produce biased estimates of baited trap fishing parameters.

La méthode de marquage–recapture a été utilisée pour mesurer le champ d'attraction et l'aire effective de pêche d'un casier appâté. Les conditions expérimentales requises pour la détermination de ces deux paramètres sont, respectivement, que les animaux marqués ne se déplacent pas et qu'ils se comportent comme des animaux non perturbés, avant d'être exposés à l'odeur de l'appât. Ces deux conditions sont possiblement contradictoires. Des observations de terrain et des expériences *in situ* ont été réalisées sur la côte nord du golfe Saint-Laurent, en 1988 et 1989, afin de comparer le comportement de buccins (*Buccinum undatum*) non perturbés à celui de buccins marqués. De jour, ~75 % des buccins non perturbés étaient au repos, partiellement enfouis et orientés de façon aléatoire, ou immobiles et orientés dans le sens du courant, alors que les autres se déplaçaient perpendiculairement au courant à des vitesses variant de 2 à 5 cm·min^{-1}. Par contre, > 97 % des buccins marqués s'éloignaient en moyenne de 2,2 à 9,2 m de leur site d'implantation en moins de 6 h, dans des directions non aléatoires et à des vitesses comparables ou supérieures à celles des buccins non perturbés. Puisqu'aucune des deux conditions essentielles n'est satisfaite, les estimés des paramètres de pêche d'un casier réalisés à partir d'expériences de marquage–recapture seraient biaisés.

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Tag–recapture methods have been used to measure the field of attraction and effective area of baited traps for gastropods and crustacean decapods in coastal environments (Ito et al. 1981; Brêthes et al. 1985; Himmelman 1988; McQuinn et al. 1988). The *field of attraction* of a baited trap is a physical area within which at least some animals actively move towards the trap in response to the odour plume from the bait. The shape and area of the field of attraction are determined by advective and diffusive processes and by chemosensory thresholds of target species (e.g. Sainte-Marie and Hargrave 1987). The *effective area* fished by a baited trap was defined by Miller (1975) as a theoretical area within which the probability of capturing all individuals of a target species is 100%. The effective area may be different from the area of the field of attraction because the proportion of animals responding to bait may decrease with distance from bait and because some trapped animals may originate from beyond the field of attraction.

In tag–recapture experiments performed by McQuinn et al. (1988), whelks (*Buccinum undatum*) were collected, tagged, and released in groups at selected points along evenly spaced transect lines radiating from a central baited trap. The number and origin of recaptured individuals were then used to determine the effective area and/or the shape and area of the field of attraction of the baited trap. An important condition for the use of tag–recapture methods to resolve the field of attraction of a baited trap is that tagged animals do not move prior to responding to the odour plume from the trap, as noted by Miller (1985). Indeed, any substantial movement would lead to questionable estimates of the shape and area of the field of attraction because (i) it would be very difficult to determine the position of a tagged animal at the time of response to bait odour, unless the direction and rate of movement were known, and (ii) tagged animals may enter the field of attraction from beyond while moving randomly or directionally. In contrast, determination of the effective area fished by a baited trap requires that a different and possibly conflicting condition be met: tagged animals must behave as undisturbed animals, which may be quiescent, move randomly, or implement specific search patterns which favour the detection of bait scent. Neither of these conditions was stated, nor tested, in previous works.

TABLE 1. Site, date, time of start of experiment, delay in hours before (−) or after (+) slack tide, and state of tide (F, flow, E, ebb) at start of dispersal experiments with tagged whelks in the Mingan Archipelago.

Experiment	Site	Date	Start	Delay	State
1	Anse-des-Noyés	July 24, 1988	13:22	−1	F
2	Anse-des-Noyés	July 29, 1988	12:30	−0.25	E
3	Anse-des-Noyés	Aug. 8, 1988	10:25	+1	E
4	Anse-des-Noyés	Aug. 9, 1988	17:03	0	F
5	Île-du-Fantôme	July 26, 1989	06:50	+0.5	E
6	Île-du-Fantôme	July 27, 1989	06:50	−0.5	E

Yet the tagging, transplantation, translocation, and/or clumping of gastropods may result in them behaving very differently from undisturbed gastropods (Petraitis 1982; Chapman 1986). McQuinn et al. (1988) noted that trap-collected whelks which were tagged in the laboratory exhibited "a period of stress-induced inactivity after release," as previously reported by Hancock and Urquhart (1959). Himmelman (1988) and McQuinn et al. (1988) concluded that this behaviour was anomalous and that it resulted in underestimates of the effective area of a baited trap. To reduce stress and increase representativity of tagged whelks relative to undisturbed whelks, McQuinn et al. (1988) suggested that whelks should be diver-collected near the experimental site and tagged in the field.

A series of tag–recapture experiments was started in 1988 to consider various aspects of whelk behaviour in the vicinity of baited traps. Because diver collection was unpractical for my large-scale experiments, whelks were trap-collected but rapidly tagged in the field to minimize disturbance. During the first tag–recapture experiment, however, SCUBA divers noticed that groups of tagged whelks cohesively dispersed from their point of release, apparently upstream, despite the absence of bait or natural carrion in that direction. This behaviour contrasted sharply with that of undisturbed whelks at the same sites, which appeared to be static or to move slowly, and could thus lead to biases in estimates of the field of attraction and effective area. Therefore, in situ experiments were designed to determine if the behaviour of tagged whelks was anomalous and, if so, to what extent it was predictable given changing environmental conditions. The specific hypotheses were that (i) undisturbed whelks move across-stream (i.e. 90 and/or 270° headings relative to standardized current direction), as this search pattern maximizes ground coverage per unit time for a scavenger or predator relying on olfaction for the detection of food (Sainte-Marie 1986), and (ii) tagged whelks released in groups move cohesively and upstream from the point of release, in the absence of bait.

Materials and Methods

Study Sites, Collection of Whelks, and Experimental Protocol

Field work was carried out at two sites in the Mingan Archipelago, Gulf of Saint Lawrence. The first station (50°13′10″N, 63°35′95″W) was located in Anse-des-Noyés, Île-du-Havre, on a flat expanse of coarse sand mixed with pebbles and rocks with scattered large boulders 10 m deep. The second station (50°14′65″N, 63°42′80″W) was located west of Île-du-Fantôme on a flat bottom of very fine sand with occasional small rocks 11 m deep. A stake and a current meter, separated by 30 m, were installed at each station. Current meters recorded mean temperature (2.5–8.5°C during experiments), current velocity, and current direction 1 m above bottom every 2 min.

TABLE 2. Mean (a) and angular deviation (s) of orientation (in degrees true north) of undisturbed whelks relative to standardized current direction (0°) in the Mingan Archipelago. The z-statistic is used to test the null hypothesis that whelks are oriented in random directions. ns, not significant; $*P < 0.05$; $*** P < 0.001$.

	Buried	Static	Moving
a	129.5	14.7	112.5
s	60.0	86.3	89.8
z	2.0 ns	9.7***	3.3*
N	6	94	38

The behaviour of undisturbed whelks was assessed by SCUBA diving before or after slack tide in Anse-des-Noyés on August 16 and 18, 1989, and off Île-du-Fantôme on August 3, 11, and 14, 1989. Up to three bottom surveys were conducted at each site to determine the behaviour of whelks, characterized as upside down, static, buried, or moving. Whenever possible, SCUBA divers using an underwater compass recorded the orientation of undisturbed moving, static, and buried whelks. The speed of several undisturbed moving whelks was also recorded.

SCUBA diving was also used to determine the behaviour of tagged whelks in the absence of bait. Fourty or 50 tagged whelks were released at the stake by SCUBA divers just after or slightly before slack tide, during daylight hours (Table 1). SCUBA divers left the site immediately after releasing the tagged whelks and returned after ~15–100 min to make two or three surveys within the next ~2–4 h. Each survey consisted of a careful inspection of the grounds immediately surrounding (≤2 m) the stake and of several circles of increasing radius, using a slightly bouyant 20-m nylon rope marked every 0.5 m and attached to the stake 0.5 m from the ground. The radius of each circle depended on visibility. The position of tagged whelks was recorded in relation to the stake using the marked rope and an underwater compass.

Whelks used in experiments were collected from the Île-du-Fantôme site in traps baited with herring protected in 1-mm Nitex mesh bags. Only whelks with undamaged shells ≥70 mm in height were used in experiments. Whelks were tagged with a rubber band and masking tape wound tightly around the shell, as described by Himmelman (1988) and McQuinn et al. (1988). Whelks were out of the water for no more than 1 min during tagging operations. There was no mortality during trapping, holding, or tagging operations. All dispersal experiments were performed within 1 d of whelk capture.

Treatment of Data

Because current direction varied during surveys and among surveys and sites, current direction at the time of observation of an undisturbed whelk was standardized to 360°, and direction of the whelk was corrected accordingly (e.g. current direction = 245.5 + 114.5°; whelk direction = 50 + 114.5°). Mean direction and angular deviation were calculated using descriptive statistics developed for circular distributions (Batschelet 1981). The null hypothesis that whelks oriented uniformly (i.e. in random directions) was tested against the alternative hypothesis of nonuniform orientation, using Rayleigh's test (Batschelet 1981). The hypothesis that whelks moved in a given direction was tested with confidence intervals for mean whelk direction, derived from charts in Batschelet (1981).

Four variables describe movement of tagged whelks away from the stake in dispersal experiments. Absolute distance (i.e. amount of movement) is a conservative estimate of total distance travelled by whelks, calculated by trigonometry assuming a straight-line trajectory between points of observation. Relative distance (i.e. displacement) is the distance separating a whelk from the central stake. Relative and absolute directions are the headings of whelks away from the stake or the previous point of observation, respectively. The center of mass of tagged whelks was calculated following equations in Batschelet (1981).

Results

Behaviour of Undisturbed Whelks in the Absence of Bait

There were no differences among surveys in the frequency distributions of whelk behaviour in Anse-des-Noyés (two surveys; G-test, $P > 0.1$) or off Île-du-Fantôme (three surveys; G-test, $P > 0.1$). Most undisturbed whelks were static (63% of 27 observations in Anse-des-Noyés and 67% of 165 observations off Île-du-Fantôme), while fewer were moving (26 and 23%) at 2–5 cm·min^{-1}, buried (4 and 8%), or upside down (7 and 2%). Behaviour of undisturbed whelks did not differ between sites (G-test, $P > 0.1$). However, the relative frequency of buried individuals was probably underestimated because whelks may bury very deeply in soft sediments and remain undetected (pers. obs.; P. Jalbert, pers. comm.; Younker and MacWilliams 1971). Siphons of static and buried whelks generally protruded from beneath the shell or sediment and occasionally swung from side to side.

Buried whelks were oriented randomly, while static whelks were oriented nonrandomly in a downstream direction (Table 2). Visual inspection of the circular frequency distribution of the direction of moving whelks suggested a unimodal pattern, apparently centered on a 110° heading, rather than a diametrally bimodal pattern centered on 90 and 270°. Statistical analysis confirms that moving whelks were not randomly oriented (Table 2), and the hypothesized 90° heading lies within the 95% confidence interval of mean whelk direction.

Behaviour of Tagged Whelks in the Absence of Bait

A number of tagged whelks were unaccounted for during all but one survey (Table 3). This was due mainly to adverse diving conditions (current velocity, extreme turbidity), as in survey 1 of experiment 5, and/or to the inconsistent diving experience of survey teams. Moreover, some uncensused tagged whelks moved beyond the range of our survey rope in less than 5 h; others were presumably hidden from sight below algae. One tagged whelk was deeply buried into the sediment (0.36% of 280 individuals), but its protruding, long, and highly visible tag made it very conspicuous; it seems unlikely that many more were buried but unnoticed. During dispersal experiments, only one tagged whelk was observed feeding; the prey item was the echinoid *Echinarachnius parma*.

TABLE 3. Mean of time elapsed between beginning of experiment and observation of tagged whelks (in min) and of relative heading (in degrees true north) and relative distance (in m) of tagged whelks in dispersal experiments conducted in the Mingan Archipelago. Mean current velocity (CV, in cm·s^{-1}) is the average of measurements between the first survey and the beginning of the experiment or between two consecutive surveys. Standard deviations are given for elapsed time and relative distance; angular deviation is given for relative heading. N is the number of tagged whelks released; N_h and N_d are the numbers of whelks used in calculations of heading and distance, respectively. The difference between N_d and N_h represents the number of whelks at the stake for which a heading could not be calculated. The z-statistic is used to test the null hypothesis that tagged whelks move away from the stake in random directions. ns, not significnt; $^{**}P < 0.01$; $^{***}P < 0.001$.

Experiment	Elapsed time	CV	Relative heading	Relative distance	N_h/N_d	z
1 (N = 50)						
Survey 1	28 ± 9	2.4	224 ± 63	1.4 ± 1.0	34/37	10.04***
Survey 2	123 ± 11	2.8	293 ± 34	6.4 ± 4.1	36/39	25.21***
Survey 3	206 ± 13	3.6	307 ± 33	7.7 ± 6.3	22/24	15.72***
2 (N = 50)						
Survey 1	33 ± 11	4.0	200 ± 103	1.9 ± 1.2	33/34	1.33 ns
Survey 2	118 ± 12	3.1	183 ± 96	2.2 ± 1.8	46/47	2.80**
3 (N = 50)						
Survey 1	26 ± 8	2.3	274 ± 46	2.0 ± 0.9	46/46	23.86***
Survey 2	115 ± 12	2.7	310 ± 37	6.8 ± 2.7	43/43	28.56***
Survey 3	229 ± 15	1.7	319 ± 36	9.0 ± 2.9	18/18	12.11***
4 (N = 50)						
Survey 1	40 ± 13	5.4	10 ± 45	2.7 ± 1.1	41/42	22.33***
Survey 2	146 ± 14	6.9	348 ± 24	8.4 ± 3.8	39/39	31.78***
5 (N = 40)						
Survey 1	74 ± 7	10.8	21 ± 71	2.5 ± 1.0	12/12	2.58 ns
Survey 2	162 ± 16	15.9	300 ± 79	5.7 ± 3.0	35/37	5.26**
Survey 3	269 ± 6	25.5	283 ± 48	9.2 ± 5.2	13/15	6.44***
6 (N = 40)						
Survey 1	113 ± 10	4.9	189 ± 79	2.4 ± 1.4	39/40	5.91**
Survey 2	204 ± 9	13.2	271 ± 70	3.5 ± 2.5	26/26	5.83**
Survey 3	310 ± 11	19.4	257 ± 75	6.5 ± 4.4	37/37	6.57**

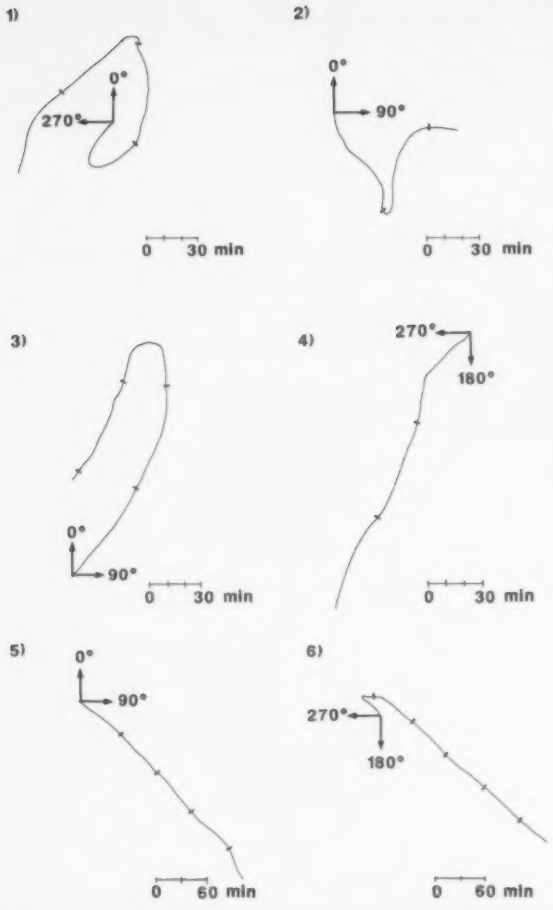

FIG. 1. Current direction during dispersal experiments in the Mingan Archipelago. The beginnings of experiments coincide with the intersection of cardinal axes; mean current direction is then plotted sequentially by 2-min intervals. Experiment numbers (Table 1) appear in the upper left corners of projections.

Overall, >97% of tagged whelks moved away from the stake before the first survey. Relative distances travelled by tagged whelks appear in Table 3. Since grounds immediately surrounding the stake were scrutinized in great detail, these mean values probably underestimate displacement. Maximum recorded relative distance was 22.5 m in 228 min, representing at least 29.3 m in absolute distance and producing a locomotory speed of at least 12.9 cm·min^{-1}. Maximum locomotory speed was ≥13.2 cm·min^{-1} by an individual which moved ≥16.1 m in 122 min.

The site off Île-du-Fantôme was characterized by a predictable diametrally bimodal flow pattern, while flow patterns in Anse-des-Noyés were unpredictable and often complex (Fig. 1 and pers. obs.). In two of six initial surveys, tagged whelks were oriented randomly around the stake, but in all subsequent surveys, tagged whelks had oriented nonrandomly (Table 3). Movement of tagged whelks was variable at a given site. In Anse-des-Noyés, the center of mass of tagged whelks was displaced 6–8 m within 2.5–4 h of the start of experiments 1, 3, and 4 but remained within 1 m of the stake during the 2-h duration of experiment 2 (Fig. 2). Off Île-du-Fantôme, the center

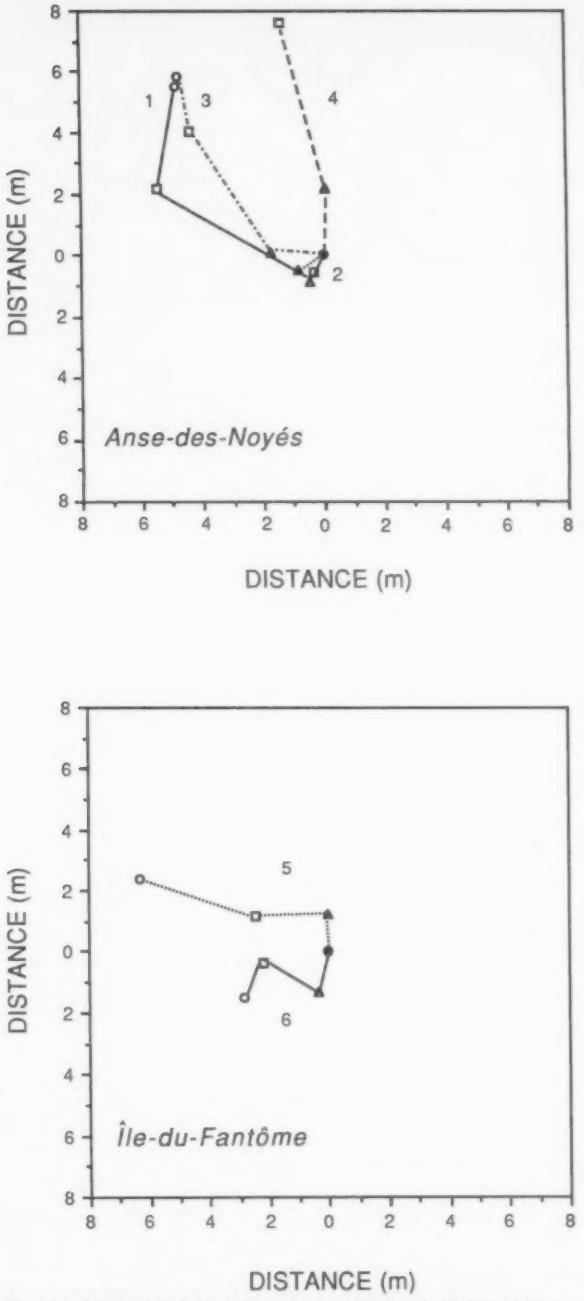

FIG. 2. Movement of the center of mass of tagged whelks relative to the stake in dispersal experiments (numbers in graphs) conducted in the Mingan Archipelago. The central black dot represents the stake; positions of the center of mass are shown by open triangles (first survey), open squares (second survey), and open circles (third survey). The *y*-axis lies along true south (bottom) and north (top) directions.

of mass of tagged whelks was displaced ~3 m in experiment 6 and >6 m in experiment 5 over a period of ~5 h (Fig. 2). Mean absolute heading of tagged whelks could not be consistently related to current direction and conformed to the hypothesized upstream movement only in experiment 5.

Discussion

In the daytime, at least 67–75% of whelks in the natural environment were quiescent but, nonetheless, the protruding siphons of buried individuals or the scanning siphons of static individuals suggest that they were in a receptive state. Indeed, most quiescent whelks responded rapidly to placement of bait in an upstream direction (pers. obs.), as has been reported by others (Gros and Santarelli 1986; Himmelman 1988). Fewer whelks were actively moving about the sediment surface, in a cross-stream direction as hypothesized. Cross-stream movement would benefit whelks with maximum olfactory prospection of bottoms per unit time (Sainte-Marie 1986). It is unclear, however, why only the 90° heading was favoured by moving whelks.

In contrast with the predominantly quiescent behaviour of undisturbed whelks, >97% of tagged whelks moved away from release points, at average speeds equalling or exceeding those of mobile undisturbed whelks. Furthermore, movement of tagged whelks was directed and uniform but, given the extent of my sampling, was unpredictable on the sole basis of local current dynamics. The gastropods *Littorina unifasciata* and *Nassarius obsoletus*, when tagged and released in groups, also move away from release points and exhibit conformity in movement, but controls or tagged individuals which are released singly behave differently (Crisp 1969; Chapman 1986). Clumping per se may have a direct effect on the behaviour of whelks, as Chapman (1986) demonstrated for *L. unifasciata* by carefully controlling for the confounding effects of tagging, transplantation, and translocation. Trail following, current-borne stimuli, behavioural interactions, and selection for topographical, bathymetric, and/or microhabitat features have been evoked to explain the uniform and extensive movement of tagged individuals of several gastropod species (e.g. Jenner 1958; Crisp 1969; Gendron 1977; Byers and Mitton 1981; Petraitis 1982).

Regardless of the reason for the anomalous behaviour of tagged whelks, be it agonistic, foraging, or other responses, basic conditions for the use of tag–recapture experiments for the characterization of trap fishing parameters were clearly violated under my experimental conditions. Determination of the shape and area of the field of attraction of a baited trap with the tag–recapture method requires that tagged whelks remain stationary prior to contacting the odour plume. In my experiments, the bias resulting from the use of tagged whelks released in groups would have been consequential because displacement over 5–6 h was of the same order of magnitude as maximum distance of attraction of quiescent whelks to baited traps, i.e. 10–22 m as determined by SCUBA divers (V. Lapointe and B. Sainte-Marie, in prep.). Moreover, because bait scent is propagated by currents, one may expect displacement of tagged whelks, before contact with the odour plume, to vary with location of release points around the baited trap.

In contrast with exigencies for the evaluation of the field of attraction, determination of the effective area fished by a baited trap with the tag–recapture method requires that tagged whelks behave as undisturbed individuals. This was not the case in my experiments, since >97% of tagged whelks moved compared with ≤26% moving undisturbed whelks. Baited traps used in a tag–recapture experiment would thus have exploited groups of shifting, uniformly oriented whelks; in the real world, however, baited traps exploit a primarily quiescent whelk population, with a mobile, cross-stream component. Baited traps would thus normally attract quiescent and mobile whelks from within the field of attraction and moving whelks which enter the field of attraction from beyond.

Furthermore, movement of tagged whelks in my experiments was unpredictable and inconsistent at a given site or between sites (Fig. 2; Table 3). Considerable spatial and temporal variability in the discordant behaviour of tagged individuals of other gastropod species has also been evidenced (Underwood and Chapman 1985; Chapman 1986). Therefore, biases in trap fishing parameters arising from the anomalous behaviour of tagged whelks cannot be accounted for by a single correction factor.

The tag–recapture method cannot easily resolve both the field of attraction and the effective area fished by a baited trap, unless the target species is a "sit-and-wait strategist" which behaves normally during experimentation. This is clearly not the case for *Buccinum undatum* and probably also for a wide variety of other animals. Consequently, I have implemented another approach to investigate the behaviour of whelks in the vicinity of traps; the results of this work will be presented at a later time.

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Spatial Stability of Cutthroat Trout (*Oncorhynchus clarki*) in a Small, Coastal Stream

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Heggenes, J., T. G. Northcote, and A. Peter. 1991. Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Can. J. Fish. Aquat. Sci. 48: 757–762.

Spatial stability and local movement of a cutthroat trout (*Oncorhynchus clarki*) population were studied from winter to late summer in a small, coastal stream. The majority of the population was static and resided within a home range <22 m^2, while a small fraction of the fish apparently was more mobile. Local movement was very restricted; 32.4% of the individually marked cutthroat were recaptured within 1 m of their original capture and marking site, and 48% remained within 3 m of that site. Only 17.9% of the fish moved more than 50 m. This behaviour was stable during winter, spring, and summer and may be of adaptive significance. Fish occupying pool areas moved considerably less than fish occupying shallow habitats, indicating that pool dwellers were dominant fish.

La stabilité spatiale et les déplacements locaux d'une population de truite fardée (*Oncorhynchus clarki*) vivant dans un petit cours d'eau côtier ont été étudiés de l'hiver à la fin de l'été. La plupart des individus se déplaçait très peu, restants à l'intérieur d'un domaine vital de moins de 22 m^2, tandis qu'un petit nombre semblaient plus mobiles. Les déplacements locaux étaient très réduits : 32,4 et 48 % des truites marquées ont été recapturées à moins de 1 et de 3 m, respectivement, de l'endroit où elles avaient été capturées pour être marquées. Seulement 17,9 % des truite marquées ont été recapturées à plus de 50 m de leur lieu de marquage. Ce comportement a été stable durant l'hiver, le printemps et l'été et pourrait donc avoir une valeur adaptative. Les poissons occupant des bassins devaient être dominants, car ils se déplaçaient beaucoup moins que ceux se tenant en eau peu profonde.

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According to the basic theory of behavioural ecology, behavioural characteristics of animals have evolved because they increase the fitness of the individual exhibiting the behaviour in question, i.e. behaviour is adaptive (Krebs and Davies 1978). Thus, different migratory strategies in salmonids may be adaptations to different environments. The often spectacular salmonid migrations have generated considerable scientific enquiry, and the potential benefits and costs of such behaviour have been repeatedly considered (e.g. Northcote 1978; Harden Jones 1981). Stream residency is also a common life history strategy in salmonids, in particular for trout. However, with the exception of territoriality as a cause of density-dependent population regulation in stream salmonids (e.g. Grant and Kramer 1990), movements of stream-resident salmonids and the biological consequences of this behavioural strategy have attracted considerably less interest. Some studies on wild stream-resident trout have indicated their movement to be quite limited (e.g. Shuck 1945), but little quantitative information is available. In wild cutthroat (*Oncorhynchus clarki*), some valuable work has dealt with homing and home territories (Miller 1954, 1957), but no accurate quantitative data are available on local movements of individual cutthroat over a long period of time. Previous studies of brown trout (*Salmo trutta*) movements in streams have focused on possible effects of fish density (Mense 1975; Heggenes 1988). In view of the several other parameters which may affect fish movements, such as their size, stream habitat, discharge pattern, and temperature regime, studies of stream movement over an extended period of time are of considerable interest, also with respect to salmonid behavioural ecology in general.

Because of the lack of such data, we designed a study to investigate seasonal variation of cutthroat trout movement in a small stream in coastal British Columbia with a numerically dominant cutthroat trout population (Northcote and Hartman 1988). Our working hypothesis was that the cutthroat trout would move less in winter because of the low water temperatures, more in spring with increasing waterflows and higher temperatures, and less in late summer at low flows.

Study Area

The Musqueam–Cutthroat Creek system (approximately 730 ha) was chosen for the study. The creek drains relatively undis-

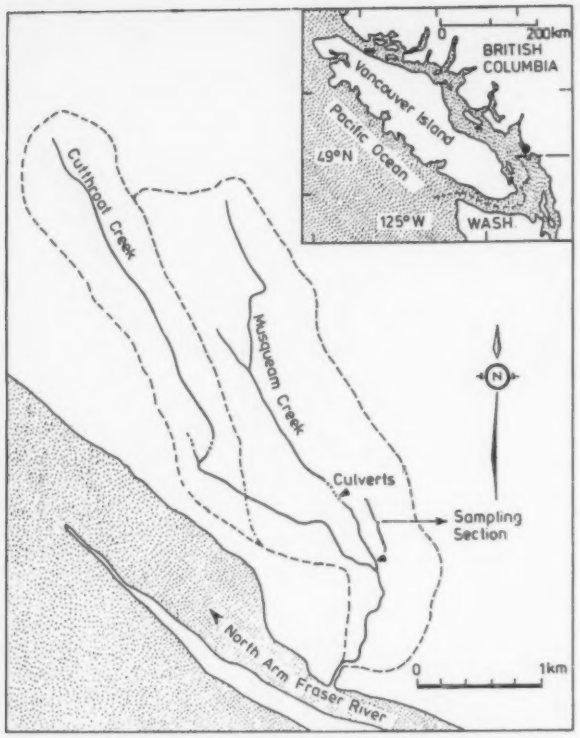

FIG. 1. Study area of Musqueam Creek, British Columbia, Canada. The extremities of the stream area studied are indicated by arrows. Inset shows the general location of the study stream.

turbed second-growth forest (Fig. 1). Much of the drainage is in glaciomarine and till deposits overlain by raised beach sands and gravels (Armstrong 1956). The uplands slope gradually up to maximum elevations about 130 m above sea level. Mean (± SD) stream width at base flow is 2.6 ± 0.9 m (range 1.2–5.5 m). Maximum stream discharge (approximately 6.5 m^3s^{-1}) occurs in late autumn to winter (Anonymous 1981), with minimum flows as low as 0.0002 m^3s^{-1} in summer to early autumn. Winter water temperatures occasionally fall below 1°C and in summer may rise above 20°C in the lowermost reaches; further upstream they are lower. The water is acidic (pH 5–6.8), with conductivity as high as 122 $\mu S \cdot cm^{-1}$ in Musqueam Creek proper during summer flow. A highway culvert in Musqueam Creek proper apparently has prevented anadromous fishes from gaining access to its upper reaches. This movement barrier represented the upper limit of the study area. Another road culvert 529 m downstream represented a large habitat shift as the creek below this culvert was channelized and very slow flowing (<5–10 $cm \cdot s^{-1}$) and was therefore chosen as the lower limit of the study area. Juvenile coho salmon (*Oncorhynchus kisutch*) occur regularly in the study area, but in low numbers compared with cutthroat trout (about 10–20% of all fish over 1 yr old). Western brook lamprey (*Lampetra richardsoni*) and prickly sculpin (*Cottus asper*) were only captured on a few occasions.

Methods

The study area was divided into 175 segments by making transects every 3 m along the stream. Transects were marked

TABLE 1. Substratum particle size classification system (modified Wentworth scale) used to categorize the Musqueam Creek streambed.

Substrate type	Size (mm)	Class
Organic fine materials		1
Organic coarse materials		2
Clay, silt	0.004–0.06	3
Sand	0.07–2	4
Fine gravel	2.1–8	5
Gravel	8.1–16	6
Small pebble	16.1–32	7
Pebble	32.1–64	8
Small cobble	64.1–128	9
Cobble	128.1–256	10
Large cobble	256.1–384	11
Boulder	384.1–512	12
Large boulders	>512.1	13
Smooth bedrock		14
Rough bedrock		15

in the field with numbered sticks and used as reference for observation of fish positions and also habitat description. Cutthroat trout were collected with a square wave pulsed DC backpack fish shocker (425 V, pulse width 6.5 ms, frequency 70 cycles per second). The anode was a 15-cm-diameter, wand-mounted ring, with an effective capture radius of about 0.5–1 m. Each captured fish >95 mm total length was marked individually with a colour marking code using a Pan Jet inoculator and Alcian blue (Hart and Pitcher 1969; Pitcher and Kennedy 1977) and released at the same position where it was captured. A specific survey procedure of upstream "point" electrofishing which reduces driving effects (Baltz et al. 1982; Hearn and Kynard 1986) was used to capture cutthroat trout and indicate their position. The anode was placed at one to three points along each transect, depending on stream width, rather than dragging it forward through the water. Whenever possible, the position of each fish was noted at the point of first sighting rather than at the point of capture to reduce the effects of galvanotaxis (Gatz et al. 1987) and with distance in metres measured from the nearest transect and the stream bank. Thus, all observations could be referred to "cells" described by a set of habitat variables (Bovee 1982). The study period was from January 1 through August 31, 1988. The stream was sampled at 2-wk intervals and at approximately base flow (40 $L \cdot s^{-1}$) except in late July – early August when the waterflow was about 5 $L \cdot s^{-1}$.

Habitat variables were measured in verticals every 20 cm across each transect at base flow. Stream width, and at each point total water depth, mean water column velocity (at 0.6 times total water depth), substratum particle size, and cover were measured. Widths and depths were measured to the nearest centimetre. Water velocities were measured with a Marsh–McBirney 201 EM water current meter fitted with a 3-cm-diameter measuring head. The dominant streambed material size was visually classified according to a modified Wentworth scale (Table 1). The mean (index of coarseness) and standard deviation (index of heterogeneity) of substrate size for each cell were computed from the recorded values according to Bain et al. (1985). Cover was estimated by viewing a rope from above. The rope was divided into 20-cm segments and was stretched perpendicular to the current along each transect. The percentage of the rope that was hidden from a view (in 10% increments from <10 to >90%) was estimated. Cover was defined as and classified into (1) submerged large organic debris, (2) other submerged structures beneath which fish could hide from view

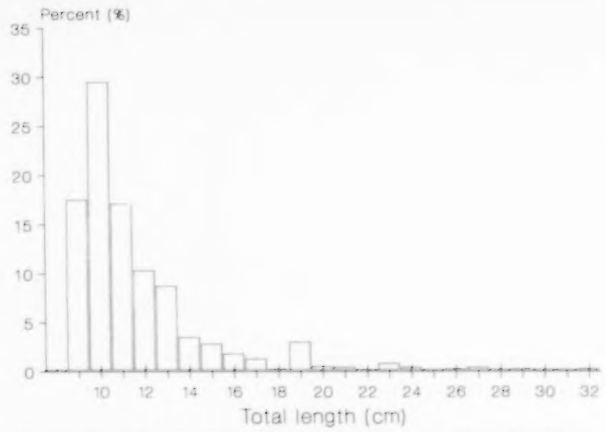

FIG. 2. Total length distribution of cutthroat trout studied in Musqueam Creek, January–August 1988.

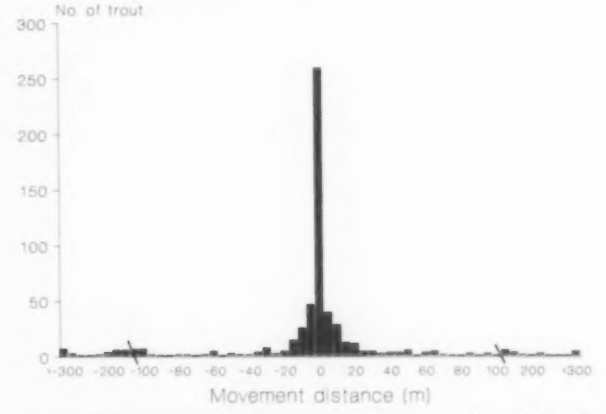

FIG. 3. Distribution of cutthroat trout movements for fortnightly periods in Musqueam Creek during winter, spring, and summer (pooled data). Each block represents a distance of 5 m for movements ≤ 100 m and a distance of 25 m for movements > 100 m. − = downstream, + = upstream.

overhead, (3) stones or boulders, (4) undercut banks or (5) overhanging vegetation less than 50 cm above the water surface, (6) broken water surface, and (7) fine organic debris.

Results

Local Movements

During the entire study period, a total of 413 cutthroat trout of varying lengths (Fig. 2; mean length = 121 mm, SD = 34) were individually marked within the study area, and a total of 754 observations were made of marked and unmarked fish. In all, 587 recaptures were made of marked trout; 246 cutthroat trout were recaptured one or more times, 147 were recaptured two times or more, 88 three times, 43 four times, 29 five times, 15 six times, 11 seven times, 7 eight times, and 1 individual was recaptured nine times during the study.

Movement of the cutthroat trout generally was very limited (Fig. 3). At least 32.4% of the recaptures did not indicate any significant movement at all (i.e. < 1 m), 48% of the recaptures were made within 3 m of last site of observation, and 63.2%

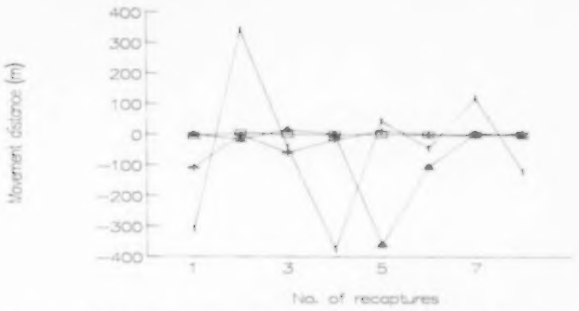

FIG. 4. Individual movement behaviour of four cutthroat trout that were recaptured eight times during the study period. − = downstream, + = upstream.

of the recaptured fish had not moved more than 10 m. Only 17.9% of the marked fish had moved more than 50 m. There were many observations near the mean relative to a normal distribution with the same mean and variance. Furthermore, due to fewer observations in the intermediate range, and some longer movements which made the tails of the distribution heavy (leptokurtosis; $g_2 = 3.1295$ of the moment statistics), a hypothesis of normality was rejected ($P < 0.001$, Shapiro Wilkes test). The mean movement distance was −5 m (SD = 78.9, $n = 587$), while the median was 0. This reflected a slight skewness of the distribution (Fig. 3) in a downstream direction ($g_1 = -0.2966$ of the moment statistics). The average time elapsing between each recapture was 31 d.

Home Range

The movement behaviour indicated that the majority of the individual cutthroat trout tended to have a small home range in the stream. Most (52%) moved less than 4 m, which would correspond to a stream area < 22 m^2 (mean area of 10.5 m^2) at base flow. The high percentage (32.4%) of trout recaptured in the same site as they were marked suggested that this was a common behaviour. No definite changes were evident in the movement pattern of fish that were recaptured several times. The mean distance moved between subsequent captures of cutthroat trout that were recaptured from two to eight times did not deviate significantly from the movement pattern of the rest of the fish ($P > 0.2550$, Kolmogorov–Smirnov test). Individual movement behaviour, however, varied greatly (Fig. 4). Most of the individuals recaptured repeatedly usually were caught on the same stream site, but in some cases a few trout moved considerable distances between recaptures (Fig. 4). Thirty-two of the individuals that were recaptured two or more times, and that had moved more than 4 m away from the site of original capture ($n = 99$), had homed and were later recaptured in exactly the same site as their earlier capture. Some of the trout apparently reestablished a new home range, or else had an extraordinarily large or a moving home range (mean area of 52.5 m^2), because 14 individuals were recaptured two or more times in two different stream reaches that were a minimum of 20 m apart. Some six individuals displayed a more transient behaviour (exemplified by one individual in Fig. 4), moving relatively long distances, and apparently without establishing any definite home range.

An analysis of movement pattern made by plotting cumulative percent of the movement observations against distance moved on a probability scale (Stott 1967) indicated that there

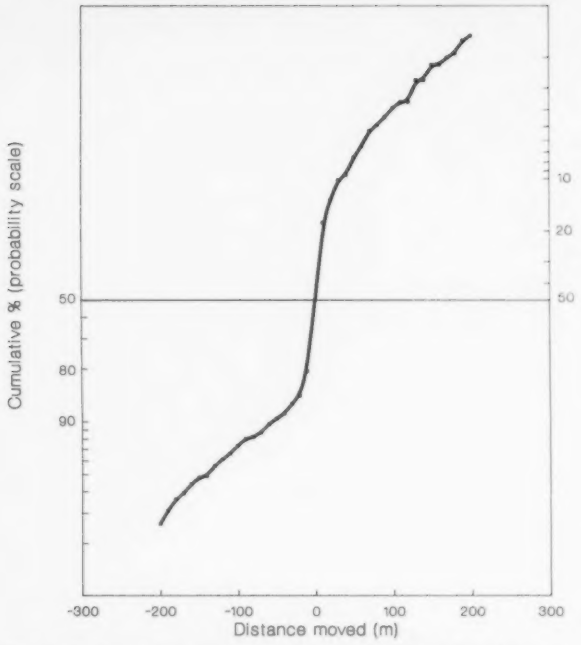

FIG. 5. Cutthroat trout movement distance plotted as a cumulative percentage of the movement observations on a probability scale.

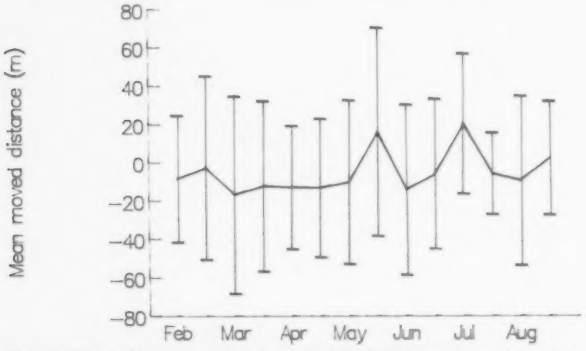

FIG. 6. Mean distance moved by recaptured cutthroat trout since their last capture. Vertical bars indicate standard deviations.

were two basically different mathematical distributions of movement within the cutthroat trout population. The sigmoid curve (Fig. 5), as contrasted with a a straight line which would have resulted from a normal distribution, suggests the superimposition of two different distributions (Solomon and Templeton 1976), one representing a large static and the other a small mobile fraction in the trout population. This fits well with the more detailed analysis of movement by individual fish (Fig. 4).

Temporal Variation in Movement Behaviour

The data were examined for temporal variation in movement behaviour by successively comparing distance moved by fish at consecutive sampling occasions from February until the end of August. Mean movement distances on the different sampling occasions (Fig. 6) suggested some change in extent of movements over the year, perhaps with less movement in winter at

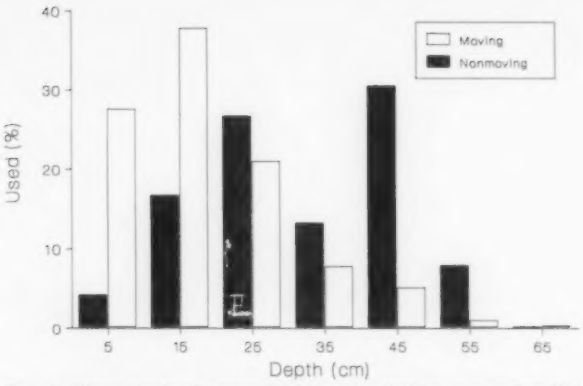

FIG. 7. Water depth of stream habitats occupied by nonmoving fish compared with initial water depths used by moving cutthroat trout before they moved (here, habitats occupied previous to movement).

low water temperatures, more movement in spring at high flows and increasing water temperatures, and less movement at low flows in late summer. However, when movement pattern obtained on each sampling occasion was compared with the pattern from the pooled data of the other fish, there was no statistically significant variation ($P > 0.1352$, Kolmogorov–Smirnov test) in movement pattern which could be correlated with either water temperature or waterflow. The one exception was for fish recaptured in late August ($n = 90$), when a trend towards slight upstream movement (mean = 2 m, SD = 59.7) ($P < 0.0001$, Kolmogorov–Smirnov test) was evident. The apparently aberrant movement behaviour which occurred in late May ($n = 25$, mean movement distance = 16 m, SD = 108.8) and early July ($n = 38$, mean = 20 m, SD = 73.2975) was caused by two outlying observations on each occasion. These were both fish of median size moving upstream. They were not physically different from the other fish in any detectable way. If these outliers were omitted, no significant changes in movement behaviour occurred.

Data were also compared individually for each sampling occasion and pooled if not significantly different. This procedure produced a basically similar result. If the two outlying observations for the late May and early June samples were omitted, no changes in the movement behaviour occurred ($P > 0.1562$, Kolmogorov–Smirnov test) over the study period, with the exception of late August.

Effect of Fish Size

Correlation between distance moved and fish length ($n = 246$) was examined by linear regression. A significant positive correlation was found ($P > F = 0.0039$), but it was very low ($R^2 = 0.0333$). Thus, fish length did not explain much of the observed variation in movement behaviour. Other factors were apparently more important.

Effect of Habitat

Data for cutthroat trout occupancy of habitat before and after movement were compared for different distance ranges in order to investigate if there was any effect of habitat on movement behaviour. Cutthroat trout that did not move (distance < 1 m, $n = 190$) occupied habitats which were different from habitats inhabited by the rest of the fish ($n = 397$). Nonmoving fish selected considerably deeper stream areas (mean water depth

= 31 cm, SD = 14) compared with fish that moved, both previous to (mean water depth = 18 cm, SD = 11) ($P < 0.0001$, Kolmogorov–Smirnov test) (Fig. 7) and after movement (mean = 22 cm, SD = 15) ($P < 0.0001$, Kolmogorov–Smirnov test). The difference also was consistent if compared with subgroups of fish that had moved different distances (>100, >50, >25, >10, and >5 m, respectively). Previously nonmoving individuals that made a subsequent movement also occupied significantly more slow-flowing habitats previous to movement (mean = 11 $cm \cdot s^{-1}$, SD = 11) than did the rest of the fish (mean = 12 $cm \cdot s^{-1}$, SD = 11) ($P < 0.0001$, Kolmogorov–Smirnov-test) and selected stream areas with more cover (mean class = 6.3, SD = 2.9 compared with mean class = 4.3, SD = 3.3) ($P < 0.001$, G-test) and slightly coarser substrate (mean class = 6.5, SD = 2.6 compared with mean class = 6.2, SD = 2.4) ($P < 0.001$, G-test). These latter differences, however, were much less pronounced, and only cover was consistently different when tested against the same subgroups that had moved different distances ($P<0.001$, G-test). Results from examination of habitats occupied after movement also indicated that the nonmoving individuals tended to use more slow-flowing habitats with more cover than did the rest of the trout.

Discussion

Previous studies of stream-living brown trout have indicated the extent of movement to be relatively limited (Shuck 1945; Allen 1951; Bohlin 1978). Miller (1954, 1957) reported movements of interior resident cutthroat trout to be restricted to a few hundred metres in a small foothills stream. Coastal cutthroat trout in the present study were spatially stable and generally showed considerably less movement that previously reported (Miller 1957). Detailed analysis of their movement behaviour in Musqueam Creek showed movements to be very restricted, usually $\leq$ 3 m, and rarely $\geq$ 50 m. Although most fish stayed in the same stream locality most of the time, individual movement patterns varied. The present results also indicate substantially less local movement by cutthroat trout than was reported in a detailed study of brown trout (Heggenes 1988). This may be a species difference. However, the brown trout study focused on somewhat larger fish, was implemented in a larger stream, and fish density was increased experimentally. Although only a low correlation was found between fish length and movement distance for Musqueam Creek cutthroat trout, this was probably due to the rather limited range of fish sizes that were studied.

The slight skewness in a downstream direction for the cutthroat movement distribution was also reported by Heggenes (1988) for brown trout. We suggest that there may be at least two reasons for this. A sudden, long upstream movement by some fish and then a passive downstream drifting over a longer time period, as was indicated by Miller (1957), can produce a negatively skewed distribution, particularly if the study section is not very long. Also, in the present study, upstream movement was prevented by a physical obstruction, as was the case in the brown trout study (Heggenes 1988). Fish drifting or actively moving downstream also would produce a negative skewness in such a situation. However, during repeated electrofishing surveys upstream from the upper culvert in Musqueam Creek, only one cutthroat trout was captured, indicating that very few downstream-moving fish entered the study area from upstream. Thus, this last explanation seems unlikely.

Brown trout resident in streams have been reported to spend most of their life within a restricted home range (Bohlin 1977, 1978; Bachman 1984). Miller (1957) suggested that each cutthroat trout in Gorge Creek had a home territory not over 18 m long. Our data suggest that the majority of home ranges for coastal cutthroat trout are much smaller, but it may be of significance that Gorge Creek was a larger stream than Musqueam Creek. Bachman (1984) reported brown trout to have individual home ranges of 15.6 m^2 in mean size, which fits well with our results. The behaviour of some of the cutthroat trout in Musqueam Creek (Fig. 4) also suggests that home ranges are not necessarily fixed to a definite stream area for every fish. It may be that some fish change and adapt their home ranges somewhat depending on environmental conditions. This is apparently contrary to findings by Bachman (1984) for brown trout, but he only studied trout living in pool-like stream areas. We suggest that a small fraction of coastal cutthroat trout may be more transient, without a definite home range, as was reported for brown trout by Jenkins (1969). A study of another brown trout population has indicated that it may consist of a large static and a small mobile fraction (Solomon and Templeton 1976). In Musqueam Creek, some proportion of the cutthroat trout is likely to be anadromous. It could be that anadromous spawners were the ones moving long distances, and thus making up part of the small mobile fraction. We were unable to tell which fish were anadromous, although the larger fish are likely to be. However, we found only a weak positive correlation between fish length and distance moved, and large resident trout were still in the stream in late summer after spawners would have left. Therefore, at least a substantial proportion of the mobile fraction of the population consisted of residents.

Variation in life history patterns appears to be adaptive, depending on the biotic and abiotic environmental conditions (Stearns 1976, 1980). There is evidence that different migratory strategies in brown trout may be adaptations to different types of habitats (Jonsson 1985, 1989). The spatial stability and movement pattern found for cutthroat trout in the present study may be of adaptive significance. In a relatively stable environment, a large static fraction of trout in the population may be expected, on the grounds of "owner's advantage" (Jenkins 1969; Bohlin 1977). We suggest that exploratory behaviour exhibited by a small mobile fraction ensures a certain amount of spatial flexibility in the population. In the face of loss of individual fish and spatial habitat disturbances, the vacant or new habitat niches will soon be occupied.

Our working hypothesis that the fish would move less in winter because of the low water temperatures, more in spring with increasing waterflows and higher temperatures, and less in late summer at low flows had some support. There was a slight trend towards less movement in winter, more in spring, and less at low flows in summer. But overall, a seasonal stability of the spatial distribution in Musqueam Creek was observed. The movement pattern found in late August was difficult to interpret. If this pattern resulted from a redistribution of fish after minimum flows in late July and early August, the change in movement behaviour might have been expected to be evident during the early part of the extreme low-flow period when the fish presumably changed location, but this was not the case in our data. Furthermore, the slight increase in upstream movement was not caused by early spawners entering the creek. However, a major problem is that the considerable variation in individual movement behaviour of some fish makes it difficult

to detect differences by conventional statistical techniques, in spite of the fact that most fish had very restricted movements.

The close relationship between selected habitat, particularly water depth, and fish movements is consistent with a cost-minimizing, linear dominance hierarchy of individuals, which has been indicated as a common social structure for stream trout populations (Jenkins 1969; Bachman 1984). Dominant individuals would be expected to select habitats affording maximum potential energy profit (Fausch 1984), and these individuals would also be expected to move less, as such movement is energetically costly in a lotic environment. Thus, older (larger) fish may have smaller home ranges (Bachman 1984). In Musqueam Creek the fish residing in the deeper stream areas, i.e. pools, were the most stationary, and thus presumably the dominant individuals.

Acknowledgements

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Allometric Scaling of Light Absorption and Scattering by Phytoplankton Cells

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Agustí, S. 1991. Allometric scaling of light absorption and scattering by phytoplankton cells. Can. J. Fish. Aquat. Sci. 48: 763–767.

Examination of the allometric scaling of light absorption (a_{cell}) and scattering (b_{cell}) by 28 phytoplankton species showed that light absorption is scaled to the cross-sectional area of the cells (log a_{cell} (square micrometres per cell) = $-1.06 + 2.32 \log d$ (micrometres)) whereas light scattering is scaled to their volume (log b_{cell} (square micrometres per cell) = $-1.09 + 3.45 \log d$ (micrometres)). The scaling of light absorption to the cross-sectional area of algal cells is explained by a decrease in intracellular chlorophyll *a* concentration as cell size increases, thereby avoiding inefficient light capture by photosynthetic pigments. The scaling of light scattering to cell volume conforms to the general theory for large particles (Mie theory). Light absorption by phytoplankton cells, unlike light scattering, deviates from that of nonliving particles because of the covariation between pigment content and cell size that help prevent self-shading.

L'examen de l'échelonnage allométrique de l'absorption ($a_{cellule}$) et de la dispersion ($b_{cellule}$) de 28 espèces phytoplanctoniques a révélé que l'absorption s'échelonne en fonction de l'aire transversale des cellules (log $a_{cellule}$) (micromètres carrés par cellule) = $-1{,}06 + 2{,}32 \log d$ (micromètres)), tandis que la dispersion s'echelonne en fonction de leur volume (log $b_{cellule}$ (micromètres carrés) = $-1{,}09 + 3{,}45 \log d$ (micromètres)). L'échelonnage de l'absorption en fonction de l'aire transversale des cellules algales s'explique par le fait que la concentration de chlorophylle a intracellulaire baisse à mesure que la cellule grossit, de sorte que les pigments photosynthétiques ne captent pas de lumière inutilement. L'échelonnage de la dispersion de la lumière en fonction du volume cellulaire concorde avec la théorie générale concernant les particules de grande taille (théorie de Mie). L'absorption de lumière par les cellules phytoplanctoniques, contrairement à la dispersion, diffère de l'absorption par des particules non vivantes car la co-variation existant entre la teneur en pigment et la taille cellulaire contribue à ce que les celllules ne jettent pas d'ombre sur elles-mêmes.

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The single best descriptor of phytoplankton ecology appears to be algal cell size, which constrains phytoplankton metabolic and ecological characteristics (cf. Malone 1980) to the point of constraining the abundance of phytoplankton species (Agustí and Kalff 1989; Agustí et al. 1987, 1990). Thus, there is a growing interest in the development of allometric scaling models that relate algal cell size to relevant physiological and ecological characteristics of phytoplankton. Available allometric models allow order-of-magnitude prediction of phytoplankton composition (cf. Reynolds 1984), growth rates (e.g. Banse 1976, 1982; Nielsen and Sand-Jensen 1990), nutrient cell quotas (Shuter 1978), photosynthetic and respiration rates (Taguchi 1976; Banse 1976), and maximal densities (Agustí et al. 1987).

Light absorption and scattering by phytoplankton are phenomena of great ecological importance because light absorption by phytoplankton constrains their photosynthetic rates and because phytoplankton contributes to, and often dominates, light extinction in lakes and oceans (Lorenzen 1972; Kirk 1980, 1983). Further, self-shading resulting from light attenuation by phytoplankton sets an upper limit to their biomass in lakes and the ocean (Steemann-Nielsen 1962; Talling 1971). Light absorption and scattering by phytoplankton cells are also expected to scale with cell size because light absorption and scattering are cell properties depending, among other factors, on the cross-sectional area of phytoplankton cells (Kirk 1983; Morel and Bricaud 1986).

Although light absorption and scattering by phytoplankton have been exhaustively studied through the application of optical theory, there are, as yet, no allometric models describing the scaling of light absorption and scattering to cell size. Such models, however, would contribute significantly to our ability to model phytoplankton and pelagic dynamics from allometric scaling models, which are becoming increasingly useful as recent instrumental developments (e.g. flow cytometer, microphotometric analysis) shift the unit of analysis from bulk community to individual cells and particles (e.g. Iturriaga et al. 1988).

Here I analyzed an extensive compilation of literature data to describe the scaling of light absorption and scattering by individual phytoplankton cells to cell size using the allometric model

$$(1) \quad Y = ad^b$$

where Y represents the light absorption or scattering of individual cells and d represents their equivalent spherical diameter (cf. Peters 1983). I then discuss the ecological implications of the resulting allometric models and interpret them in light of available theoretical models derived from the application of optical laws (cf. Kirk 1975a, 1975b, 1976; Morel and Bricaud 1981).

Methods

To obtain the broad ranges in cellular and optical characteristics necessary to achieve my goals, I searched the available literature for data on optical properties (i.e. absorption and scattering coefficients and efficiencies) and cellular characteristics (i.e. cell size and chlorophyll *a* content). The data set compiled comprises 28 (34 cultures), largely marine, phytoplankton species ranging widely in cellular and optical properties (Table 1) and grown under light intensities ranging from saturating to limiting (Table 1). Because the methods used to derive the optical characteristics differed among studies (opal glass and integrating sphere, Table 1), I used analysis of covariance (ANCOVA) to test for any systematic bias attributable to differences in optical techniques on the relationships examined. Because light absorption and scattering are spectral properties, I simplified the analysis by focusing on absorption and attenuation measured at 675 nm. This wavelength corresponds to peak absorption by chlorophyll *a*, where absorption measurements are least influenced by absorption due to pigments other than chlorophyll *a*, and is the wavelength most often reported in the literature.

The allometric model (Eq. 1) was fitted to the data using major axis regression analysis, following logarithmic transformation of dependent and independent variables (Till 1974; LaBarbera 1989), to avoid bias in the equation coefficients derived from measurement error. The power of these relationships was described by the percent variance in optical properties accounted by algal cell size (R^2), and their precision was described by the standard error of the regression estimates.

Recalculation of reported optical characteristics (often chlorophyll *a* specific coefficients) were based, when necessary, on the Beer law. This law states that light absorption (a) at wavelength λ is proportional to the concentration (C) of the light-absorbing substance according to the expression

$$(2) \quad a = a^* C r$$

where r is the pathlength of light through the medium (standardized to 1 m) and a^* is the specific absorption coefficient of the substance. This law applies also to the calculation of attenuation (c) and scattering (b) coefficients:

TABLE 1. Optical and cellular characteristics of the phytoplankton species used in this analysis. I, irradiance (μeinsteins$\cdot m^{-2}\cdot s^{-1}$); d, modal cell diameter (μm); Chl, cellular chlorophyll *a* content (pg); c_i, intracellular Chl *a* concentration (pg$\cdot\mu m^{-3}$); a_{cell} and b_{cell}, absorption and scattering, respectively, by individual cells ($\mu m^2\cdot cell^{-1}$). λ = 675 nm.

Species	I	d	Chl	c_i	a_{cell}	b_{cell}	Source[a]	Method
Cricosphaera carterae	150	10.00	1.200	0.0023	13.56	—	1	Integrating sphere
Cricosphaera carterae	5.6	13.50	4.650	0.0036	32.55	—	1	
Cricosphaera carterae	5.6	11.30	6.670	0.0088	60.03	—	1	
Thallassiosira eccentrica	150	32.30	13.900	0.0008	148.73	—	1	
Scrippsiella trochoidea	5.6	19.70	3.940	0.0010	52.80	—	1	
Nannochloris sp.	150	2.50	0.130	0.0159	1.91	—	1	
Platymonas suecica	400	6.00	0.540	0.0048	11.90	—	2	Opal glass
Coccolithus huxleyi	400	3.80	0.030	0.0010	0.86	—	2	
Chaetoceros protuberans	400	26.50	1.050	0.0001	33.72	—	2	
Chlorella pyrenoidosa		1.78	0.185	0.0626	0.80	—	3	Sample in front of
Chlorella pyrenoidosa		1.84	0.136	0.0417	0.90	—	3	the photomultiplier
Chlorella pyrenoidosa		1.66	0.086	0.0359	0.65	—	3	
Chlorella pyrenoidosa		1.60	0.067	0.0312	0.66	—	3	
Chlorella pyrenoidosa		1.58	0.073	0.0353	0.65	—	3	
Chlorella pyrenoidosa		1.68	0.075	0.0302	0.71	—	3	
Hymenomonas elongata	300	11.50	2.340	0.0029	46.82	163.88	4	Opal glass
Platymonas sp.	300	7.40	0.390	0.0018	13.89	71.42	4	
Tetraselmis maculata	300	9.50	0.720	0.0016	21.82	120.00	4	
Coccolithus huxleyi	300	3.40	0.020	0.0010	0.68	11.96	4	
Chaetoceros curvisetum	400	7.50	0.290	0.0013	6.86	70.68	5	Opal glass
Chaetoceros lauderi	400	25.50	2.770	0.0003	61.12	577.87	5	
Pavlova pinguis	400	3.60	0.106	0.0043	1.80	16.22	5	
Pavlova lutheri	400	4.50	0.125	0.0026	2.63	39.88	5	
Primnesium parvum	400	5.70	0.250	0.0026	3.72	55.85	5	
Dunaliella salina	400	10.20	3.420	0.0062	35.94	135.20	5	
Porphiridium cruentum	400	4.90	0.260	0.0042	4.01	42.93	5	
Synechococcus sp.	400	1.60	0.005	0.0022	0.09	0.47	5	
Synechocystis sp.	200	1.50	0.003	0.0014	0.05	0.41	5	
Synechocystis sp.	16	1.50	0.004	0.0023	0.11	0.52	5	
Thalassiosira sp.		5.14	0.400	0.0056	7.48	47.60	6	Integrating sphere
Clone 2601		4.11	.110	0.0030	3.56	28.88	6	
Nannochloris atomus		3.66	0.090	0.0035	2.31	0.71	6	
Synechococcus "Syn"		1.47	0.002	0.0012	0.08	0.28	6	
Synechococcus WH7803		1.21	0.001	0.0011	0.05	0.06	6	
Minimum		1.21	0.001	0.0001	0.05	0.06		
Maximum		32.3	13.9	0.0626	148.73	577.87		
Average		7.34	1.296	0.0095	16.87	72.88		

[a]Sources: (1) Haardt and Maske (1987); (2) Morel and Bricaud (1981); Privoznik et al. (1987); (4) Bricaud et al. (1983); (5) Bricaud et al. (1988); (6) Osborne and Geider (1989).

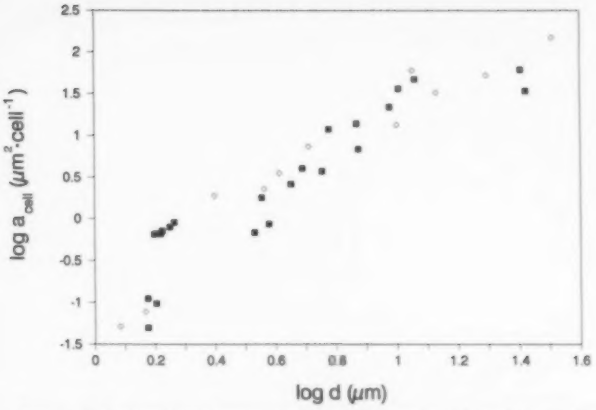

FIG. 1. Relationship between the modal diameter (d) and the light absorption by individual phytoplankton cells (a_{cell}). Symbols represent measurements derived using opal glass (■) and integrating sphere (◇).

(3) $c = c^* C r$

(4) $b = b^* C r$

where c^* and b^* are the specific attenuation and scattering coefficients of the substance, respectively. In addition, the specific coefficients also fulfil the equality

(5) $c^* = a^* + b^*$

where a^*, b^*, and c^* are usually used to refer to the specific absorption, scattering, and attenuation coefficients of in vivo chlorophyll a, respectively. The absorption, scattering, and attenuation coefficients of the individual algal cells (denoted here as a_{cell}, b_{cell}, and c_{cell}, respectively) were calculated from the specific coefficients using Eq. 2, 3, and 4 where C represented the cell concentration in the suspension.

The dimensionless parameters Q_a, Q_b, and Q_c, describing the efficiency of the light absorbed, scattered, and attenuated, respectively, by the cross-section of a particle, are defined as

(6) $Q_a = 2/3\ a^*\ c_i\ d = 4\ a^*_{cell}/\pi\ d^2$

(7) $Q_b = 2/3\ b^*\ c_i\ d = 4\ b^*_{cell}/\pi\ d^2$

(8) $Q_c = 2/3\ c^*\ c_i\ d = 4\ c^*_{cell}/\pi\ d^2$

where c_i represents the intracellular chlorophyll a concentration, and also fulfil the equality

(9) $Q_c = Q_a + Q_b$.

Results

Scaling of light absorption by individual algal cells to cell size accounted for most of the >1000-fold variation observed in light absorption by algal cells (Fig. 1). The slope of the allometric equation between light absorption by algal cells (a_{cell}) and cell diameter (d) indicated (Eq. 10, Table 2) that light absorption by phytoplankton cells is proportional to their cross-sectional area (i.e. d^2; H_0: slope = 2, $P > 0.05$). Thus, small algae absorb more light, relative to their volume, than larger algae (Fig. 2). Notably, cyanobacteria exhibit a substantially lower light absorption relative to their cell volume than algae from other taxa similar in size (Fig. 2). However, the relationship between a_{cell} and cellular chlorophyll a content (Fig. 3; Eq. 11, Table 2) was almost linear (H_0: slope = 1, $P > 0.05$) and significantly stronger than that between a_{cell} and cell size (Fig. 1; Eq. 10, Table 2), as well as unrelated to taxonomic position of the algae. Thus, scaling of light absorption by individual phytoplankton cells to their cross-sectional area appears to derive from the fact that the cellular chlorophyll a content is also scaled to the cross-sectional area (Eq. 12, Table 2). Similarly, the lower absorption per unit volume of cyanobacteria

TABLE 2. Regression equations describing the relationships between optical properties of phytoplankton and the size or pigment content of the cells. Regression coefficients were derived by fitting the equation $\log y = a + \log x$. Also provided are the coefficient of determination (R^2) and the standard error of the slope (SE_{slope}) and of the regression estimates ($SE_{log\ estimate}$). d, modal cell diameter (μm); Chl, cellular chlorophyll a content (pg); a_{cell} and b_{cell}, absorption and scattering, respectively, by individual cells (μm^2·cell^{-1}). λ = 675 nm.

y	x	a	b	R^2	SE_{slope}	$SE_{log\ estimate}$	Equation
a_{cell}	d	−1.06	2.32	0.88	0.18	0.34	10
a_{cell}	Chl	1.17	0.92	0.94	0.05	0.22	11
Chl	d	−2.42	2.52	0.78	0.29	0.32	12
b_{cell}	d	−1.09	3.45	0.93	0.18	0.27	13
b_{cell}	Chl	2.28	1.14	0.94	0.05	0.24	14

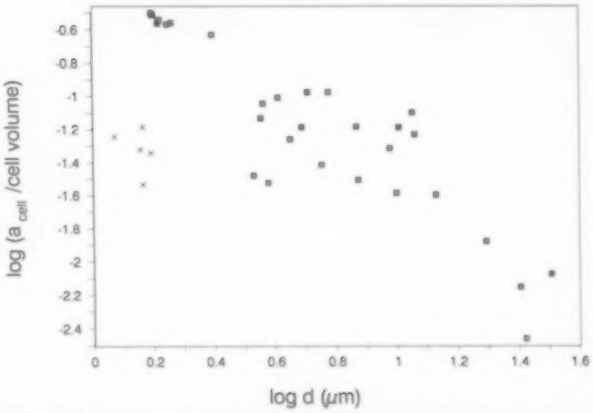

FIG. 2. Relationship between the modal diameter (d) and the ratio of cell absorption to cell volume (a_{vol}) of phytoplankton cells. Symbols represent cyanobacteria (×) and algae from other taxa (■).

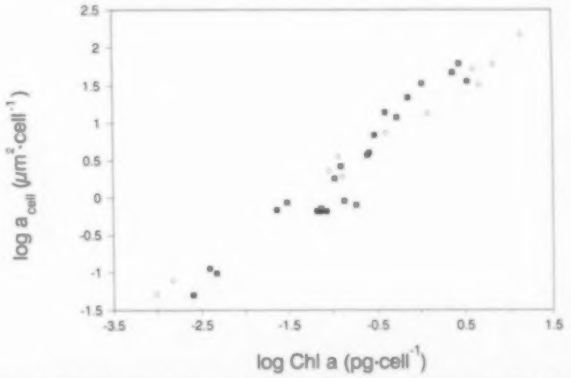

FIG. 3. Relationship between the chlorophyll a content and the light absorption by individual cells (a_{cell}) of phytoplankton. Symbols as in Fig. 1.

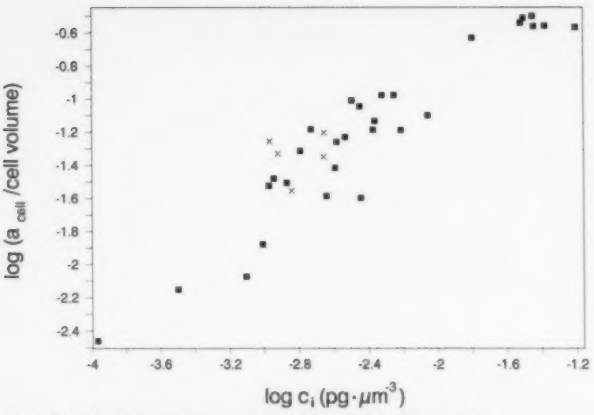

FIG. 4. Relationship between the intracellular chlorophyll *a* concentration (c_i) and the ratio of cell absorption to cell volume (a_{vol}) of phytoplankton cells. Symbols represent cyanobacteria (×) and algae from other taxa (■).

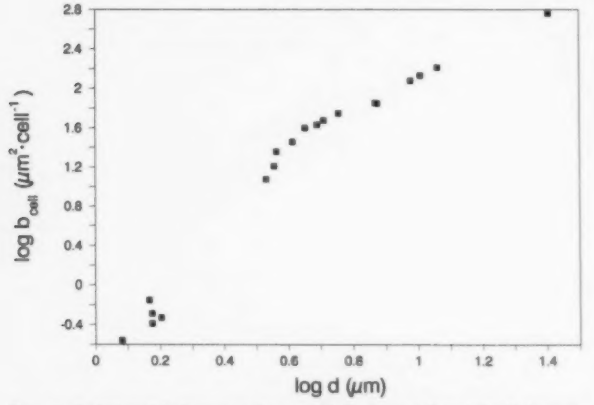

FIG. 5. Relationship between the modal diameter (d) and the light scattering by individual phytoplankton cells (b_{cell}).

relative to other taxa with similar size (Fig. 2) is a consequence of the lower intracellular chlorophyll *a* concentration of cyanobacteria, as demonstrated by the similarity in the scaling of light absorption per unit cell volume (a_{vol}) to the intracellular chlorophyll *a* concentration of cyanobacteria and algae from other taxa (Fig. 4).

The magnitude of light scattering and attenuation (675 nm) by individual cells was strongly correlated ($r = 0.99$, $P < 0.0001$; Table 1) because light attenuation by phytoplankton was largely dominated by scattering, which was, on average, eightfold greater than light absorption (Table 1). Light scattering by individual algal cells was strongly correlated with the size ($R^2 = 0.93$; Fig. 5) and chlorophyll *a* content ($R^2 = 0.94$; Fig. 6) of the algal cells. The allometric equation (Eq. 13, Table 2) describing the scaling of light scattering by individual algal cells (b_{cell}) to cell size (d) shows that light scattering by phytoplankton cells is scaled to their volume (H_0: slope = 3, t-test, $P > 0.05$) and not, unlike light absorption (Eq. 10, Table 2), to their cross-sectional area. The relationship between light scattering by phytoplankton cells and the cellular chlorophyll *a* content (Eq. 14, Table 2) was similarly strong, but almost linear. Because of the dominance of scattering in light

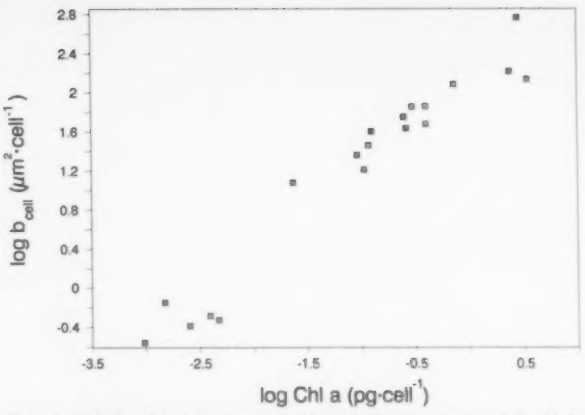

FIG. 6. Relationship between the chlorophyll *a* content and the light scattering individual phytoplankton cells (b_{cell}).

attenuation by phytoplankton, light attenuation showed a similar scaling to cell size and chlorophyll *a* content than that of light scattering (Fig. 5 and 6).

The relationships described were all independent of the method used to measure *a*, *b*, and *c* (ANCOVA, $P > 0.05$), indicating that differences among methods had no systematic effect on the scaling of light absorption and scattering to cell size (Table 1).

Discussion

The allometric analyses of light absorption by individual algal cells indicated that, as expected from theoretical models (Morel and Bricaud 1986), the light absorbed by phytoplankton cells is scaled to their cross-sectional area (Fig. 1; Eq. 10, Table 2). Thus, algal cells absorb less light, relative to their volume, as they increase in size (Fig. 2). However, the scaling of light absorption by phytoplankton cells to their cross-sectional area derives from the fact that chlorophyll *a* content of the cells is scaled to their cross-sectional area. This conclusion is based on (1) the linearity and greater precision of the relationships between the chlorophyll *a* content of phytoplankton cells and their absorption of light and between the absorption per unit cell volume and the intracellular chlorophyll *a* concentration of the algal cells (Fig. 4) and (2) because models based on chlorophyll *a* content and intracellular concentration explain the apparently deviant behaviour of blue-green algae in models based on cellular size alone (cf. Bricaud et al. 1988).

The scaling of the chlorophyll *a* content of phytoplankton cells to their cross-sectional area (Eq. 12, Table 2) implies that their intracellular chlorophyll concentration (i.e. pigment packaging) decreases with increasing cell volume (Bricaud et al. 1988). The observed scaling of chlorophyll *a* cellular content and intracellular concentration to cell size has an important adaptive value because it avoids the inefficient light absorption by increasingly self-shaded pigments that would develop if the intracellular concentration were constant regardless of cell size (cf. Kirk 1975a, 1975b).

In addition, the linear relationship between light absorption by individual algal cells and cell chlorophyll *a* content (Eq. 11, Table 2) implies, in agreement with experimental data describing changes in light absorption and pigment content of cells grown under diverse irradiances (e.g. data for *Cricosphaera*

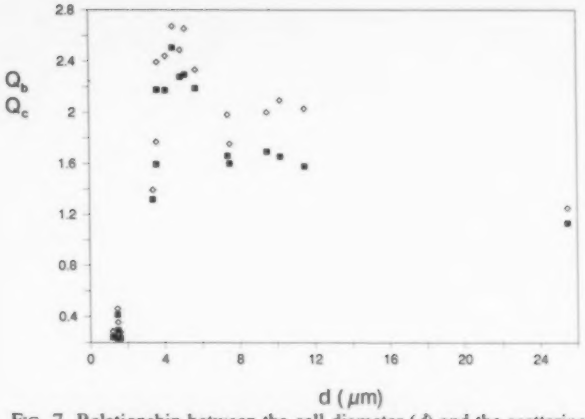

FIG. 7. Relationship between the cell diameter (d) and the scattering (Q_b, ■) and attenuation (Q_c, ◇) efficiency of phytoplankton cells.

carterae in Haardt and Maske (1987); Table 1), that the higher chlorophyll *a* content of algae grown under low irradiances should result in a proportional increase in the light they absorb. Thus, the results presented here also allow a simple description of algal photoadaptation to low irradiances, which often involves an increased chlorophyll content (Steemann-Nielsen and Jørgensen 1968).

The present results also show that phytoplankton contributes largely to light attenuation (about 90% on the average) through light scattering (Bricaud et al. 1983; Bricaud and Morel 1986), both of which are scaled to the cell volume and the chlorophyll *a* content of phytoplankton cells (Eq. 13 and 14). In addition, the size dependence of the scattering and attenuation efficiency of phytoplankton cells conforms to general models of scattering by large (greater than wavelength) particles (Fig. 7; Mie theory, cf. Bricaud and Morel 1986). Thus, small (<5 μm) cells absorb more light and scatter less light, relative to their volume, than larger cells and must, therefore, be better competitors under light-limited situations.

In summary, the results obtained reveal the existence of allometric relationships between algal size and relevant phytoplankton characteristics (1) yielding models that allow coarse predictions of the light absorbed and scattered by phytoplankton cells from cell size and (2) offering interpretations of the coefficients of the allometric models, obtained on the basis of the allometric scaling of pigment content and intracellular concentration, that are in accord with optical models (Kirk 1986; Morel and Bricaud 1986). Light scattering by phytoplankton is very similar to that by nonliving particles. However, the present results demonstrate that light absorption by phytoplankton deviates from that of nonliving particles because of a covariation between pigment content and cells size which prevents self-shading.

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Population Dynamics and Food Habits of Bluegill (*Lepomis macrochirus*) in a Thermally Stressed Reservoir

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Taylor, B. E., J. M. Aho, D. L. Mahoney, and R. A. Estes. 1991. Population dynamics and food habits of bluegill (*Lepomis macrochirus*) in a thermally stressed reservoir. Can. J. Fish. Aquat. Sci. 48: 768–775.

Bluegill (*Lepomis macrochirus*) is the dominant fish species in a 67-ha cooling reservoir for a nuclear reactor on the Savannah River Site in South Carolina. Mortality and breeding season of bluegill were strongly influenced by reactor operations, which often produced temperatures of 40–60°C in portions of the reservoir. Late spring and summer reactor operations caused ~90% mortality of bluegill. This mortality was largely associated with reactor restarts. Survivors occupied small thermal refuges in coves. Elevated fall and winter temperatures allowed an extended breeding season, although extremely high summer temperatures appeared to inhibit breeding. Bluegill depended primarily on benthic food resources, including dipterans and microcrustaceans. Despite the great variation in environmental conditions and diets, body condition of surviving bluegill was nearly constant between April 1985 and January 1986. Factors that contribute to the success of bluegill in this system include high thermal tolerance, broad diets, and an ability to breed when thermal conditions are appropriate, regardless of season.

Le crapet arlequin (*Lepomis macrochirus*) est l'espèce de poisson dominante dans les eaux d'un bassin (67 ha) de refroidissement d'un réacteur nucléaire situé au site de la rivière Savannah en Caroline du Sud. Ce réacteur a accru de façon importante la mortalité du crapet arlequin et en a largement modifié la saison de reproduction. Dans certaines zones du bassin, la température de l'eau atteignait souvent 40 à 60°C. À la fin du printemps et durant l'été, le réacteur a entraîné une mortalité d'environ 90 %. Cette mortalité était largement attribuable aux remises en marche du réacteur. Les survivants se réfugiaient dans de petites baies où la température leur était plus favorable. Les températures élevées durant l'automne et l'hiver avaient pour effet d'allonger la saison de reproduction; toutefois, les températures très élevées durant l'été inhibaient la reproduction. Dans ce bassin, le crapet arlequin se nourrit surtout d'organismes benthiques, dont des diptères et des microcrustacés. Malgré les variations importantes de leur diète et des conditions environnementales, l'état physique des crapets survivants est resté presque constant d'avril 1985 à janvier 1986. La survie du crapet arlequin dans ce système est attribuable notamment à sa tolérance aux températures élevées, à son régime alimentaire diversifié et à sa capacité de se reproduire en toute saison, du moment que les conditions thermiques s'y prêtent.

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Responses of aquatic communities to altered temperature regimes are difficult to predict, whether the thermal effects are produced locally by heated effluents or regionally by climatic change. Although fish species that tolerate extreme temperatures in the laboratory are more likely to persist in extreme natural environments (Matthews 1987), laboratory data on temperature preferences only partially predict distributions in nature (Magnuson et al. 1979). For individuals, survival in a thermally stressed environment is influenced by factors such as acclimation, behavior, and nutrition, as well as thermal tolerance (Hutchison 1976). Patterns of spatial and temporal variation and trophic interaction also affect the response of the community to temperature (Larimore and Tranquilli 1981).

To determine factors contributing to the survival of bluegill (*Lepomis macrochirus*) under adverse thermal conditions in a small cooling reservoir, we investigated population dynamics, condition, and diets of the bluegill over a series of rapid and extensive temperature changes. The reservoir, Pond C, is used to cool effluent water from a nuclear production reactor on the Savannah River Site (SRS) near Aiken, South Carolina. When the reactor is operating, water temperatures (40–60°C) in large portions of the reservoir exceed lethal temperatures for fish and most other aquatic organisms. Under these conditions, fish retreat to cooler areas. Even in these refuges, fish can experience temperatures near their upper thermal tolerances (Siler and Clugston 1975; Block et al. 1984).

Methods

Study Site

Pond C is a 67-ha reservoir with maximum depth of 10 m and mean depth of ~2.5 m (Fig. 1). Heated effluent is discharged from a nuclear reactor into P Canal. The effluent travels 7 km through the canal and several small ponds before entering Pond C and then flows from Pond C into Par Pond (a 1012-ha reservoir) through a culvert under the Hot Dam. When the reactor is operating, flow rates through P Canal average 11 m^3/s, and the residence time of water in Pond C is ~1.5 d. Pond C has been receiving thermal effluent since 1958.

Fish Sampling and Diets

Numbers of fish killed during reactor operations were estimated by counting dead fish along twenty 100-m sections of

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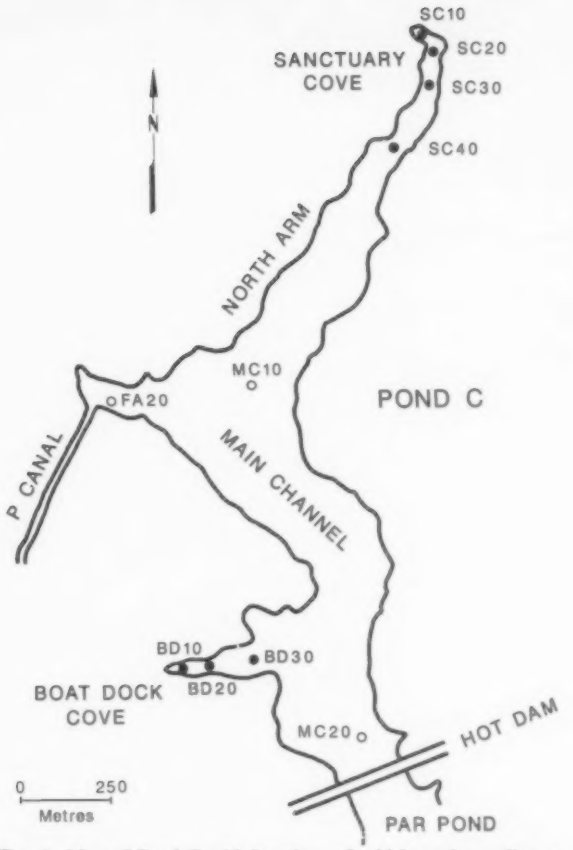

FIG. 1. Map of Pond C with locations of midchannel sampling stations. Solid circles indicate cove stations; open circles indicate main channel stations.

shoreline (total sampled length was ~28% of the perimeter of Pond C). Frequency of sampling depended on the phase of the reactor operation schedule. Counts were usually made daily for 3 d after a restart and then at 2- to 3-d intervals during the remainder of the operating cycle. The estimate of the total fish kill from the counts followed recommendations of the Pollution Committee of the American Fisheries Society (AFS 1982) and is further described in Aho and Anderson (1985).

To estimate abundances, fish populations were sampled once or twice monthly by electroshocking near shore (depth <2.5 m) at 10–12 randomly located sites in January and April 1985 and June 1985 to January 1986. All collections were made between 10:00 and 14:00 and the time (typically 2–4 min) spent at each site was recorded. All fish were measured (total length, TL) and a randomly chosen subsample were weighed (nearest gram). Fish for stomach analysis were placed on ice and frozen upon return to the laboratory. Fish from Sanctuary and Boat Dock coves, the only areas where we consistently collected fish, were used for the diet analyses presented here.

Stomach contents of bluegill from eight sampling dates were examined: 22 April 1985, n = 28 fish; 27 June, n = 20; 16 August, n = 36; 8 September, n = 18; 4 October, n = 16; 7 November, n = 26; 11 December, n = 17; 30 Janaury 1986, n = 23. Each fish used for diet analysis was measured (TL) and weighed (nearest 0.01 g). All prey were counted and identified, except in a few cases when microcrustaceans were subsampled quantitatively. The amount of bluegreen algae was evaluated on a scale of 0 (none) to 3 (very abundant).

Biomass of prey was estimated by weighing animals from Pond C (*Moina*, nematodes) or L Lake, a nearby reservoir (cyclopoid copepodids and nauplii, *Chaoborus*), or by applying published length–weight regressions to length measurements of animals from Pond C or L Lake (other cladocerans, dipterans). Except nematodes, animals to be weighed were taken from freshly collected samples and killed with dilute formalin. Nematodes were taken from preserved samples. The animals were measured, rinsed in deionized water, transferred to tared aluminum foil boats, dried at 60°C overnight, cooled in a desiccator, and then weighed to the nearest 0.1 μg with a Cahn model 31 electrobalance. Regression equations from Smock (1980) were used for dipterans, and equations from Culver et al. (1985) and Dumont et al. (1975) were used for cladocerans.

Relative body condition by date was estimated by the residuals (the difference beween actual $\log_e$ (weight) and predicted $\log_e$ (weight)) of the length–weight regression for bluegill from the electroshocking censuses. The regression equation for fish ≥75 mm was

$$\log_e(\text{weight in g}) = 3.370 \log_e(\text{TL in mm}) = 12.848$$
$$(n = 760, r^2 = 0.96).$$

Sample size by date was 10–111 fish (median = 36 fish, n = 17 dates). Initial analyses showed that the exponent of the length–weight relationship varied among dates, so that the commonly used index K (LeCren 1951), which assumes that the exponent is 3, was not appropriate.

Zooplankton Sampling

Zooplankton were sampled at 2- to 4-wk intervals from April to June 1985 and then at 1-wk intervals from July 1985 to January 1986. Samples were collected at 10 stations: seven in the coves and three in the main channel (Fig. 1). At the two deep main channel stations (MC10 and MC20), duplicate samples were taken just below the surface and at 2-m intervals to 4 or 6 m. At the remaining, shallower stations, duplicate samples were collected just below the surface and at 1-m intervals to 2 m, depth permitting. The total number of samples usually taken on each date was 16 for the main channel stations and 20–26 for the cove stations. The reservoir was sampled during midday (10:00–15:00) in spring, fall, and winter but somewhat earlier (08:00–11:00) in summer when the reservoir was very hot. Samples were collected with a 3.3-L. Van Dorn bottle, concentrated by filtering through a 50-μm-mesh sieve, and preserved with formalin and sugar. Water temperature was measured at each sampled depth. Zooplankton were stained with Eosin B and counted at 25× magnification.

Results

Our study began in April 1985 during a 50-d reactor shutdown (Fig. 2). From late May through January 1986, the reactor operated for periods of ~3–4 wk separated by short (~1 wk) shutdowns. During periods of reactor operation, the range of cove temperatures was typically 39–47°C in summer and 29–37°C in winter. The main channel was always warmer (typically 44–56°C in summer and 29–47°C in winter) than the coves when the reactor was operating. Pond C did not stratify strongly, except in the vicinity of inlet streams or seeps, because

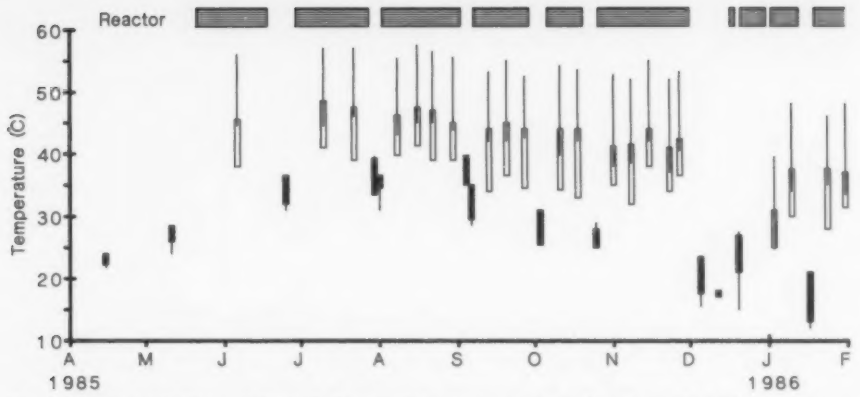

FIG. 2. Thermal conditions at Pond C. Temperature ranges are given for all samples at the seven cove stations (rectangles) and three main channel stations (vertical lines). Open rectangles indicate that the reactor was operating; solid rectangles indicate that it was not. The bar above the panel shows periods of reactor operation.

water was released to Par Pond from the bottom of the reservoir. Near the dam, the thermal gradient from 0 to 6 m (near the bottom) was typically 2° when the reactor was operating. After shutdown, water temperatures dropped quickly, but generally did not return to seasonally normal values before restart occurred. Normal surface temperatures for two nonthermal reservoirs on the SRS range from ~10°C in midwinter to ~30°C in midsummer (SREL, unpubl. data).

Shallow-water substrates along the main channel and in the coves were covered with a mat of blue-green algae, primarily *Oscillatoria*. Emergent vascular plants were found only where natural streams or groundwater entered the reservoir.

Bluegill were the most abundant fish. Mosquitofish (*Gambusia holbrooki*) are usually codominant (Aho and Anderson 1985), but were rare during most of this study. Largemouth bass (*Micropterus salmoides*) and redbreast sunfish (*Lepomis auritus*) were commonly present, but never abundant.

Size, Mortality, and Condition of Bluegill

Observations of active nests in the coves and presence of gravid females in the electroshocking samples indicated that fish were spawning in April–May 1985, and successful recruitment was indicated by the presence of very small fish (25–50 mm) in the electroshocking samples. Reproduction had apparently begun in late fall or early winter because very small fish were already present in samples in January 1985 (Fig. 3). Reproduction apparently ceased in late May after the restart of the reactor because neither nesting nor gravid females were observed. Also, very small fish were rare in the summer collections. Modal size of the bluegill population increased fairly steadily from April to December. Nesting was again observed in October and continued through January 1986, and very small fish reappeared in the samples in October.

Large numbers of dead bluegill were found after late spring and summer reactor restarts (Fig. 4). The largest fish kill occurred in May, following the 50-d reactor outage. Most fish were killed within the first week of a reactor restart, although a large number were found dead in July about 2 wk after another restart, when high winds apparently pushed hot water farther up into Sanctuary Cove. Catch per unit effort calculations from the electroshocking data indicate that the bluegill population declined by ~90% during the summer (Fig. 4). Few dead fish were found after fall and winter reactor restarts, and the population did not decrease further.

Body condition of the bluegill remained nearly constant during most of the study period (Fig. 4). Body condition was measured by deviations from the pooled $\log_e$ weight – $\log_e$ length regression for all measurements from the electroshocking censuses. Only fish collected in late June showed a substantial negative deviation from this regression. The average residual for this date was -0.39 ($n = 30$), which corresponds to a reduction of ~30% from the predicted weight. As measured by the standard deviation of the residuals, this collection also showed the greatest variation among individuals. Overall, fish condition on dates when the reactor was operating did not differ significantly from condition on dates when the reactor was not operating (Mann Whitney test, $n = 17$ sampling dates, $p > 0.05$).

We compared condition of bluegill ≥75 mm from two other sites on the SRS by calculating deviations of $\log_e$ weight from the regression equation for bluegill from Pond C. The bluegill were collected by electroshocking from L Lake, a 405-ha cooling reservoir, in September 1988 and from Par Pond, the reservoir that receives water from Pond C, in April–August 1989. Neither system has received heated effluent since spring 1988. The mean deviations were 0.000 for bluegill from L Lake (SD = 0.018, $n = 15$; R. Fletcher, SREL, unpubl. data) and -0.100 for bluegill from Par Pond (SD = 0.099, $n = 263$; M. Belk, SREL, unpubl. data).

Diets of Bluegill

Bluegill consumed a wide range of food items, including chironomids, cladocerans, copepods, ostracods, and nematodes. Fish were very rarely eaten. Mean and median numbers of animal prey per stomach for all fish were 232 and 54 (range 0–7987). No food was found in 6.5% of the stomachs. We classified fish as small (TL < 75 mm) or large (TL ≥ 75 mm), according to an approximate size criterion for behavioral and dietary shifts determined by Mittelbach (1984). Composition of the prey varied substantially among dates, size groups, and, as indicated by quartiles and ranges of the proportions, among individuals (Fig. 5). Stomachs of large bluegill contained an

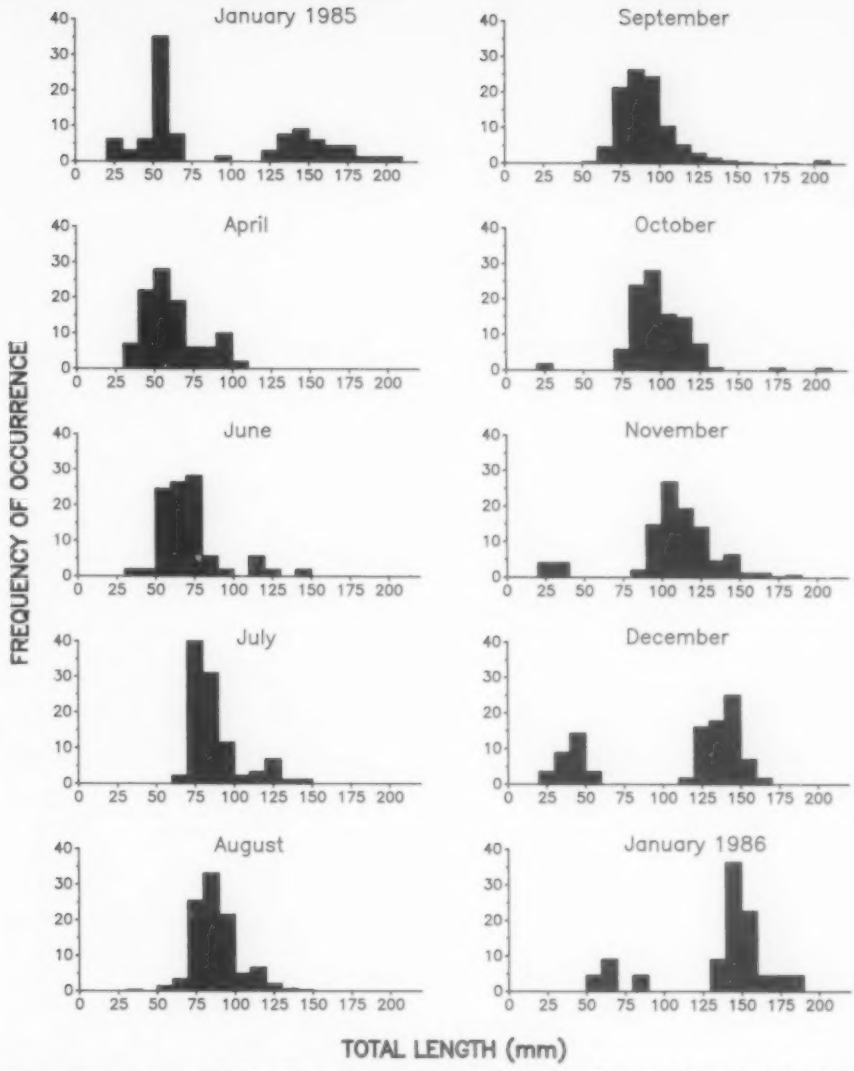

FIG. 3. Size structure of the bluegill population in Pond C. Fish were collected by electroshocking along littoral zone transects.

abundance of blue-green algae during August–November, whether the reactor was operating or not. Only in August did stomachs of small fish contain more than trace amounts of blue-green algae.

Both planktonic and benthic prey were common in the diets of small bluegill (Fig. 5). Most of the prey were crustaceans, but dipterans, other insects, and other invertebrates were also found in the stomachs. In April and June, *Bosmina* was the only planktonic cladoceran eaten; from November to January, planktonic cladocerans in the stomachs were mainly *Moina*. Planktonic cladocerans were entirely absent from the diets in August. The most commonly eaten benthic crustaceans wre chydorids, primarily *Alona*, and cyclopoid copepodids, except in June and August, when most were macrothricids. In April and June, nematodes and rotifers comprised most of the prey in the miscellaneous category; from November to January, nearly all prey in this category were nematodes.

Large bluegill consumed higher proportions of dipterans and lower proportions of benthic crustaceans and fed more heavily on other insects and larger animals (Fig. 5). The median proportion of planktonic cladocerans in diets of the large fish was >0.1 in December; the cladocerans were mainly *Moina*. Among the benthic crustaceans, macrothricids, *Alona*, and cyclopoids were abundant for large bluegill, as well as for small bluegill. Ostracods were also important for the large fish. Nearly all prey from the miscellaneous category on all sample dates were nematodes.

Prey biomass was estimated for microcrustaceans and for dipterans and nematodes (Fig. 6). Numerically, these taxa included 98% of the prey consumed. For small fish, the median proportion of microcrustacean biomass was greater than 0.5 (range 0.58–1.00) for all dates except April, when the median was 0.29. For both groups of prey, biomass was highest in April and June and low for the water sampling dates. For the large fish, the median proportion of dipterans and nematodes was >0.65 (range 0.68–0.95) on all dates. Dipterans were usually the most important prey in this group, and only large blue-

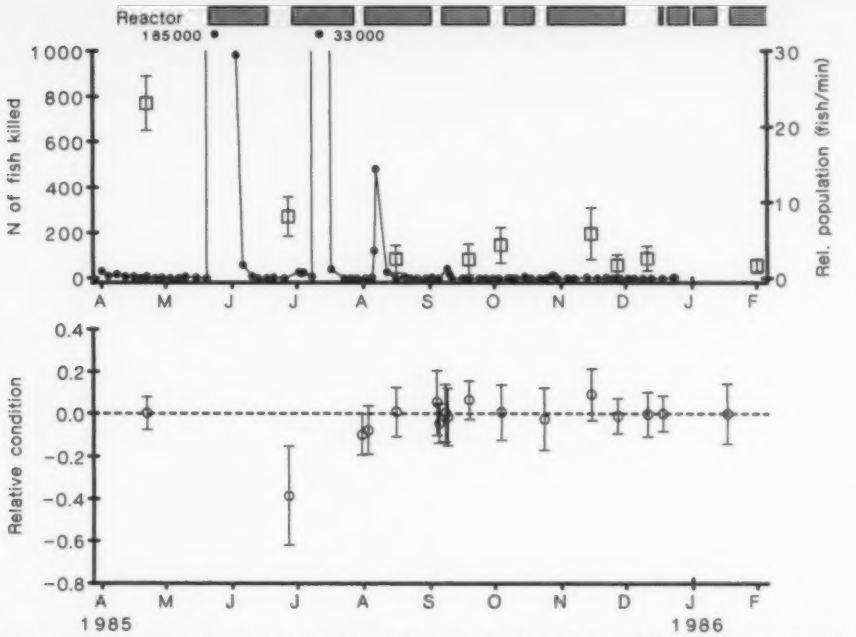

FIG. 4. Fish kills, abundance, and condition of bluegill. Number of bluegill killed (upper panel, left-hand axis, solid circles) is the estimate for the entire reservoir from counts along sections of shoreline. Relative abundance of bluegill (upper panel, right-hand axis, open squares) is measured as catch per minute obtained by electroshocking. Means were calculated from samples along 11–13 transects; bars show ± 1 SE of the mean. Relative body condition (mean ± SD, lower panel) is estimated by residuals from the $\log_e$ weight – $\log_e$ length regression. The bar above the upper panel shows periods of reactor operation.

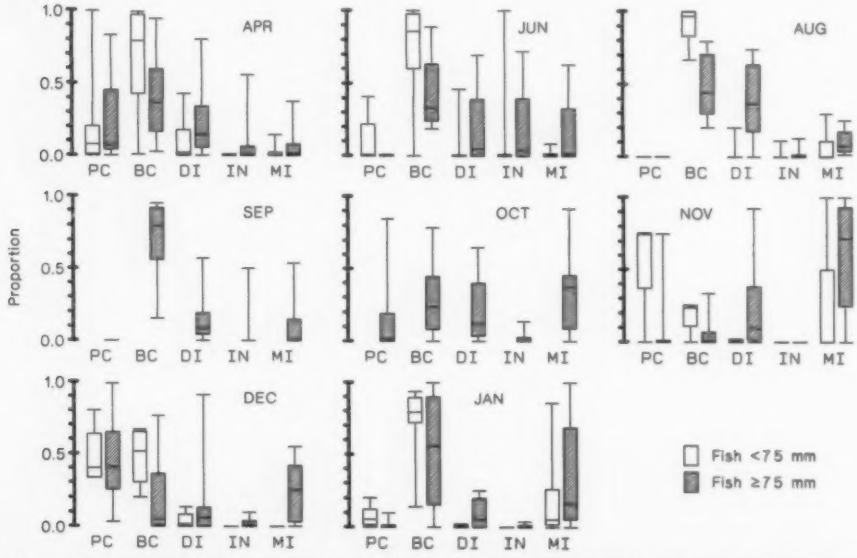

FIG. 5. Composition of bluegill diets: PC, planktonic cladocerans; BC, benthic crustaceans; DI, dipteran larvae and pupae; IN, other insects; MI, other animal prey. Medians, quartiles, and ranges of proportions are shown for small fish (TL < 75 mm) (unshaded rectangles) and for large fish (TL ≥ 75 mm) (shaded rectangles). Only fish whose stomachs included animal prey were included.

gill in November consumed a substantial amount of nematodes (median proportion of biomass = 0.11). The biomass varied widely among dates: medians were highest in April and August and lowest in September and January.

For large fish, average median prey biomass for dates when the reactor was not operating was 3.7 mg (n = 5) and was 4.0 mg (n = 3) when the reactor was operating. The difference between these values is not significant (t = −0.076, p = 0.94). For large fish, the proportion of fish with abundant blue-

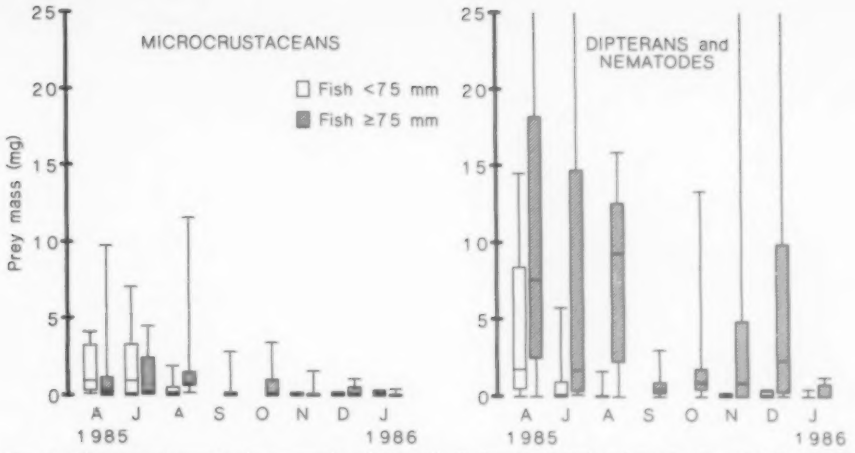

FIG. 6. Biomass of prey in the stomachs of bluegill. Estimates include microcrustaceans (planktonic cladocerans and benthic crustaceans) and dipterans and nematodes. Medians, quartiles, and ranges are shown for small fish (TL < 75 mm) (unshaded rectangles) and for large fish (TL ≥ 75 mm) (shaded rectangles). Summaries include fish with empty stomachs.

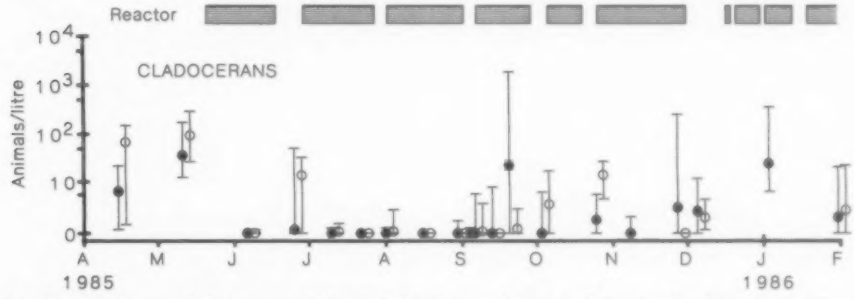

FIG. 7. Abundances of cladocerans in Pond C. Medians and ranges of average densities in the coves (solid circles) and main channel (open circles) are shown. (The main channel summary is offset slightly to the right of the sampling date.) Summaries were calculated from average densities for each depth at each station. On several dates (1 August, 20 September to 25 October), data from station MC20 were not available. The y-axis is scaled by log ($y + 1$). The bar above the panel shows periods of reactor operation.

green algae in the gut was not correlated with the median biomass of the animal prey (Spearman's rho = -0.24, $n = 8$, $p > 0.05$).

Zooplankton Community

The planktonic community at Pond C was dominated by rotifers, which were nearly always abundant (>500 animals/L) in at least some parts of the coves. Planktonic cladocerans were quite variable in abundance (Fig. 7). They were virtually absent from June through August, except during brief periods when the reactor was not operating. They were often abundant in fall, winter, and spring, whether or not the reactor was operating. The common cladocerans were two species of *Moina*, *Bosmina longirostris*, *Ceriodaphnia lacustris*, and *Diaphanosoma* sp. Cyclopoid copepods, primarily *Tropocyclops prasinus*, were also occasionally abundant.

Discussion

Mean critical thermal maxima for bluegill in Pond C range from 37.0 to 41.1°C, depending on acclimation temperature (Holland et al. 1974). Thus, during summer when the reactor was operating, high temperatures probably excluded bluegill from the vicinities of all 10 sampling stations. The fish were presumably restricted to very shallow water at the edges and ends of the coves and to cooler inflows from small streams and springs at several places in the North Arm and coves, as described by Siler and Clugston (1975) and Block et al. (1984). As temperatures declined in the fall, the refuge area increased substantially. By January, only the outfall station (FA20) was warmer than 40°C when the reactor was operating, so most of the reservoir was probably accessible to fish.

The data on fish kills suggest that late spring or summer reactor restarts imposed the greatest stress on the bluegill population. The bluegill population, estimated from the electroshocking census, declined by ~90% during May–August reactor operations in 1985 (Fig. 2). The fish kills that occurred during this period were associated with high temperatures in the coves (Fig. 2) and very small areas of refuge. The greatest numbes of dead fish were usually collected in the first week of reactor operations, suggesting that the rapid changes in temperature caused mortality. Failure to find refuge or insufficiently rapid physiological adaptation could result in death for

the fish. Perhaps because the refuge areas were larger, the fish kills associated with fall and winter restarts were minimal.

Bluegill in lakes and ponds of the southeastern coastal plain typically have a long breeding season: they can spawn from early April to mid-October (George W. Lewis, University of Georgia Cooperative Extension Service, Aquaculture and Fisheries, pers. comm.). Nesting has been observed in all months of the year at Pond C (Clugston 1973; this study). Clugston concluded that temperature, rather than photoperiod, was the proximal cue for nesting, and he observed a broad range of temperatures (17.5–37°C) in active nests. In our study, the presence of very small size classes (25–50 mm) in the population sampled by electroshocking showed that reproduction was successful in both spring and fall. Clugston observed spawning or young in nests during December, January, and February, as well as during warmer months. In our study, the rarity of very small fish indicated that reproduction was unsuccessful during the summer, perhaps due to the high temperatures in the reservoir. Clugston also observed that reproduction ceased during summer when water temperatures were high (36–42°C).

Bluegill in Pond C depended primarily on benthic food resources during our study. Dipterans comprised the bulk of the diet of large fish (≥75 mm) on all sampled dates. Except in our initial sample, during the 50-d reactor shutdown, small fish (<75 mm) fed primarily on microcrustaceans. These diets are typical of bluegill (for example, Keast 1978; Lemly and Dimmick 1982). Bluegill are generally opportunists in selection of prey (Werner et al. 1981; Mittelbach 1984). At Pond C, composition of the diets varied substantially over time, suggesting temporal changes in food resources. The occurrence of blue-green algae in the diets may indicate a reduction in abundance of animal prey (Ali and Bayne 1985). Bluegill may have been feeding on the benthic algal mat to obtain microinvertebrates associated with it, although there was no correlation between abundance or composition of prey and amount of blue-green algae in the stomachs. Bluegill probably are unable to digest most of the algal material, but may derive some nutritional benefit from it (Kitchell and Windell 1970). In an earlier study at Pond C, during a year when the reactor was not shut down for >20 d at a time, Johnson (1975) found that filamentous algae comprised >50% by weight of the stomach contents of bluegill in spring, summer, and fall.

Despite the variation in temperature and diets, body condition of the surviving bluegill was nearly constant over the study period. Condition of the bluegill at Pond C was similar to or better than condition of bluegill from two nearby reservoirs at ambient temperatures. Growth and condition have been strongly correlated with abundance of food for bluegill in other southeastern reservoirs (Lemly and Dimmick 1982). In a small cooling reservoir in North Carolina, bluegill and other sunfish became emaciated during summer when they were forced by extreme temperatures to remain in coves with a substrate of *Oscillatoria* (Graham 1974). In Pond C, the data suggest that food resources were usually not depleted for periods long enough to affect body condition. The only occurrence of low condition, which was in June, could reflect limited food resources when bluegill were forced into small refuge areas during the period of reactor operation that preceded the June fish sample. During subsequent summer periods of reactor operation, bluegill were much less numerous, reducing the potential for competition.

Cladocerans were rare in Pond C during summer reactor operations, although maximum thermal tolerances among cladocerans are similar to those among rotifers, which remained abundant (Taylor and Mahoney 1988). Cladoceran populations did increase during the short summer reactor shutdowns. After the refuge areas expanded in September, cladocerans were often abundant during reactor operations. We speculate that predation by bluegill prevented development of cladoceran populations during summer reactor operations, when the fish populations were concentrated into small refuges.

Aquatic animals at Pond C often endure conditions near the limits of their thermal tolerances. Even the most tolerant and successful species, such as bluegill among the fish and the rotifer *Filinia longiseta* among the zooplankton (Taylor and Mahoney 1988), can suffer great mortality during reactor operations. The success of bluegill at Pond C probably depends on flexibility in breeding season and diet, as well as high thermal tolerance and ability to use thermal refuges.

The composition of the community at Pond C should predict a set of potential survivors for other systems that are stressed by high temperatures. However, the extreme effects of the effluent on population densities must abruptly alter biotic interactions, such as competition and predation. Because these effects occur at short (usually ≤1 mo), irregular intervals, Pond C is unlikely to provide an adequate model for the more gradual and subtle effects of climatic change on dynamics or trophic structure of a community.

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Indirect Effects of Detritus Manipulations in a Montane Stream

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Richardson, J. S., and W. E. Neill. 1991. Indirect effects of detritus manipulations in a montane stream. Can. J. Fish. Aquat. Sci. 48: 776–783.

To evaluate the common assumption in stream ecosystem theory that fine-particle feeders can indirectly benefit from coarse-particle detritus consumed by detritivores, we manipulated whole-leaf detritus in replicated experimental stream channels. Elevated input rates of detritus resulted in significantly higher densities of collectors and moderate but nonsignificantly higher densities of predators. When collectors were analyzed as filterers and gatherers separately, there were significantly higher densities of both groups at a high loading rate of leaves. The net rates of colonization for each trophic group did not differ significantly with respect to treatment, which suggests that the increased densities of collectors observed under high leaf input rates were due to increased survival of larvae. Density of no single taxon increased significantly in response to coarse particulate organic matter inputs; rather, most species showed moderate increases. Species richness showed no treatment effect. Increases in collector density may result indirectly from increased fine particulate organic matter production due to feeding by shredders. Predaceous species which responded were small taxa and were probably predators on collectors. These effects were observed over a period of less than 5 mo and demonstrate the potential strength of the interactions.

Pour vérifier l'hypothèse selon laquelle, dans la théorie des écosystèmes des cours d'eau, les organismes se nourrissant de particules fines ("collecteurs") peuvent tirer profit des restes laissés par les détritivores se nourrissant de particules grossières, on a ajouté dans des portions de cours d'eau des détritus de feuilles entières dans le cadre d'expériences répétées. L'augmentation des détritus a accru de façon significative la densité des collecteurs et, dans une moindre mesure, statistiquement non significative, celle des prédateurs. Parmi les collecteurs, tant les filtreurs que ceux qui recherchent activement les particules fines ont vu leur densité augmenter de façon significative quand les feuilles étaient ajoutées en grande quantité. Les taux nets de colonisation des différents groupes trophiques ne variaient pas de façon significative selon le traitement, ce qui laisse entendre que l'accroissement de la densité des collecteurs suite à des ajouts importants de feuilles était attribuable à l'accroissement du taux de survie des larves. La densité d'aucun taxon n'a augmenté de façon significative suite à l'addition de particules organiques grossières; le nombre d'individus de la plupart des espèces a plutôt augmenté de façon modérée. Les traitements n'ont pas eu d'effet sur la diversité des espèces. L'accroissement de la densité des collecteurs pourraient être attribuable indirectement à l'augmentation de la production de particules organiques fines par les organismes qui déchiquètent leurs aliments. Les espèces prédatrices qui ont vu leur nombre s'accroître appartenaient aα des taxons de petite taille et s'alimentaient probablement de collecteurs. Les effets des traitements ont été observés durant moins de 5 mo et témoignent de l'importance potentielle des interactions existant entre ces organismes.

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The importance of indirect effects, i.e. interactions between species mediated through intervening species, has recently been emphasized in community ecology (Bender et al. 1984; Davidson et al. 1984; Carpenter 1988; Yodzis 1988). There are many possible indirect effects, such as apparent competition, synergistic effects between predators, and exploitative competition. Tests of these effects require detailed manipulations of the densities of particular species or other community parameters (Carpenter 1988).

One hypothesis of an indirect interaction in streams is a facilitation hypothesis based on detritivorous consumers ("shredders") of coarse particulate organic matter (CPOM) making finer particles of detritus (FPOM) available to fine-particle feeders or collectors (Cummins 1974; Short and Maslin 1977; Vannote et al. 1980). Fine particles of detritus are generated from feeding activities and defecation of shredders, physical breakdown of larger particles (Cummins et al. 1983), and flocculation of dissolved organic carbon leached from detritus (Lush and Hynes 1973). The flow of energy through shredders to collectors is an implicit and central assumption of current views of stream ecosystem function (Cummins 1974; Vannote et al. 1980). However, there is little evidence for the assertion that generation of FPOM due to detritivore feeding activities contributes to nutrition of collectors under natural conditions (Winterbourn et al. 1981). Several studies have shown that manipulations of detritivore abundance can affect concentrations of suspended and benthic FPOM (Wallace et al. 1982; Mulholland et al. 1985), but these studies did not look for an effect on collectors. Laboratory studies have shown that FPOM generated from shredder faeces is often better energetically and nutritionally for collectors than the average quality of FPOM sampled from natural streams (Short and Maslin 1977; Ward and Cummins 1979; Mattingly 1987; but see Shepard and Min-

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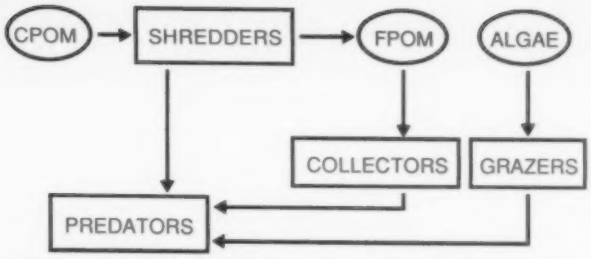

FIG. 1. Trophic web indicating the presumed connections among components of the stream community (after Cummins 1974).

shall 1984 for an exception). However, it has not been shown that the magnitude of the contribution of particles produced from shredder feeding activities can affect quality of FPOM appreciably beyond that of the background FPOM.

A second possible effect of coarse detritus manipulation is that increased productivity at one trophic level may result in increased available prey biomass for predators. These kinds of multitrophic level, "bottom-up" mechanisms have been discussed at length for lake communities in recent years (Carpenter et al. 1985; McQueen et al. 1986) but have figured little in stream literature (Bowlby and Roff 1986), although they are implicit assumptions of stream ecosystem theory (Cummins 1974; Vannote et al. 1980). If collectors of fine organic particles (FPOM) benefit from the feeding activities of large-particle detritivores, then there should be increased density (via increased survival or colonization) or growth of collector species. Invertebrate predators are predicted to exhibit aggregative increases in density within patches of high prey density. If prey availability is increased, then capture rate per predator (and hence growth rate) might increase in addition to, or instead of, increases in predator density.

Experimental additions of whole-leaf detritus to stream channels alongside a small montane stream in southwestern British Columbia have shown that populations of CPOM detritivores are strongly food limited (Richardson 1991). This experiment also provided an excellent opportunity to examine the effects of increased detrital input rates on field populations of species that do not directly consume CPOM. Many potential indirect effects are possible in this type of experiment on a variety of time scales (Yodzis 1988). This paper is concerned with those strong trophic effects that are detectable on a short (seasonal) time scale that are less likely to be averaged out by many small effects on longer time scales (Vandermeer 1990). The trophic model (Fig. 1) on which our predictions are based is from Cummins (1974).

Materials and Methods

This experiment was carried out in six parallel streamside channels adjacent to Mayfly Creek. Mayfly Creek is a second-order stream in the Malcolm Knapp Research Forest of the University of British Columbia, approximately 60 km east of Vancouver, B.C. The watershed is in the Coastal Western Hemlock zone and was logged early in this century. The stream reach near the channels has only a partial canopy, and the dominant riparian species are red alder (*Alnus rubra*), vine maple (*Acer circinatum*), western hemlock (*Tsuga heterophylla*), red cedar (*Thuja plicata*), and salmonberry (*Rubus spectabilis*). Details of water chemistry and geology for similar streams nearby in the Research Forest have been previously published (Feller and Kimmins 1979).

The experimental design and channels have been described elsewhere (Richardson 1989, 1991). Briefly, natural benthic communities were allowed to establish in the streamside channels (15 m × 35 cm) receiving water from the adjacent Mayfly Creek and allowing immigration and emigration from the channels. Discharge through each channel was very similar, but varied between dates (range 1.3 to 3.0 $L \cdot s^{-1}$) with discharge in Mayfly Creek. However, May–October was a period of fairly stable baseflow. The bottom substratum consisted of 3–4 cm of gravel and sand (<5 mm in diameter) to a depth of 20 cm, and flow created a series of riffles and pools, which were similar among all six channels. The interstitial spaces among the gravel provided habitat for macroinvertebrates, and irregularities in the gravel surface retained detritus. The average slope of the channels was 0.03.

Three treatments with two replicates each received different input rates of dried alder and vine maple leaves. Leaves were added on 10 dates between May and September 1986. One pair of channels had an input rate that mimicked the natural input rates recorded during 2 yr of sampling along Mayfly Creek (summer input rate of 80 $mg \cdot m^{-2} \cdot d^{-1}$, Richardson 1989); this is referred to as the control or "natural" treatment to differentiate it from observations in the natural stream. The high food input rate was equivalent to the peak autumnal input rate (3.2 $g \cdot m^{-2} \cdot d^{-1}$, 40 times natural summer input), and intermediate treatment streams received 720 $mg \cdot m^{-2} \cdot d^{-1}$ (9 times "natural").

Ten benthic samples were collected from each channel on 1 May 1986, and then the channels were randomly assigned to treatment. At 2-wk intervals from May to the beginning of September, five samples per stream were collected. Benthic samples were collected using a modified Surber sampler with a sampling area of 402 cm^2 and a net with mesh size of 102 μm. Samples were preserved immediately in formaldehyde solution. In the laboratory, samples were sieved into various size fractions, and all animals retained on a 471-μm sieve were separated from detritus under a dissecting microscope at 12× magnification, identified to the lowest reliable taxonomic level, and counted.

Immigration and emigration rates were measured to determine whether any differences in benthic densities were due to differential colonization or survival in the different treatments. Samples were collected for periods of 24 or 48 h using nets with mesh size 250 μm through which the entire water flow of each channel could be filtered. Samples for immigration and emigration were taken on nine occasions between May and September, but never during the 48 h after benthic samples had been taken and detritus added.

The abundance of FPOM in the particle size range 471 μm to 1.0 mm was measured as ash-free dry mass in export (emigration) and benthic samples. Particulate organic matter in this size fraction collected from the emigration samples was dried and weighed for four dates to estimate export rate of this material. We used the mass of particles in this size range as an index of FPOM export, since finer nets would have clogged too rapidly to be practical. While collectors may feed on much finer particles as well, we assumed that detrital abundance in different size categories would be positively correlated.

Emergence traps were emptied about twice a week from May to October. There were six traps (each 900 cm^2) on each stream channel. Emergent adult insects were collected in a cup fitted

with an inverted funnel placed on top of each trap. The data sets for many species were incomplete for several reasons. Dipteran adults were not examined at all, and mayfly subimagos could not be identified to species where there was more than a single species in a genus, e.g. *Baetis*. Many other taxa taken in benthic samples were seldom collected in emergence traps.

Taxa were assigned to a trophic category on the basis of data given by Merritt and Cummins (1984) and Pennak (1978). Many taxa were omitted from the density analyses because of low numbers. Many taxa are omnivorous so that trophic classification is not precise. Some taxa, i.e. *Baetis, Epeorus,* and *Paraleptophlebia*, have been variously assigned to trophic groups by different authors. Thus, analyses were performed with these particular taxa in different trophic categories to determine if their exclusion altered the results. Taxonomic resolution was determined by ease of identification or availability of diagnostic characters.

Statistics

The data were analyzed using SAS statistical software (SAS Institute Inc. 1985). We tested the benthic data from the first posttreatment sample date of the experiment (15 May 1986) to 4 September inclusive. Benthic data and immigration and emigration rates were transformed as $\log_{10}(n+1)$ and fitted to a multiway, nested, unbalanced ANOVA using general linear models (SAS Institute Inc. 1985) with date as a covariate and streams as replicates within treatments. After fitting a model using partial sums of squares (type III sums of squares, SAS Institute Inc. 1985), treatment effects were tested by dividing treatment mean squares by the mean square of replicate channels within treatments as the appropriate error term (this is equivalent to a repeated measures ANOVA), compared with an F of 2,3 degrees of freedom. In all cases the critical level of significance was $\alpha = 0.05$ corrected by the sequential Bonferroni procedure for multiple comparisons (Rice 1988). The least squares means for each stream, determined from fitting the complete ANOVA, were used in the a posteriori Tukey's test to assess treatment differences. Sign tests were used to compare the ranks of taxa within trophic categories, i.e. whether the densities tended to be higher under certain treatments.

Results

Fine Particulate Organic Matter

The quantity of FPOM exported from the channels was significantly enhanced by treatment ($F_{2,3} = 11.99$, $P < 0.04$) in the order high > intermediate > control (Fig. 2). The export rate from the channels with the highest amount of leaf material was greater than twice that of the control (Tukey's test, $P < 0.05$). There was no significant difference in benthic FPOM (471 μm to 1.0 mm) per sample related to treatment (Fig. 2, $F_{2,3} = 0.71$, $P > 0.5$).

Benthic Densities

A total of 36 taxonomic groupings of organisms, presumed not to be consumers of CPOM on the basis of Merritt and Cummins (1984) and Pennak (1978), were tested for an effect of treatment on density. Benthic densities of none of the taxa showed significant differences due to detritus manipulations (Table 1). The four taxa showing the largest effects (all nonsignificant) were Chironomini (Chironomidae), Simuliidae,

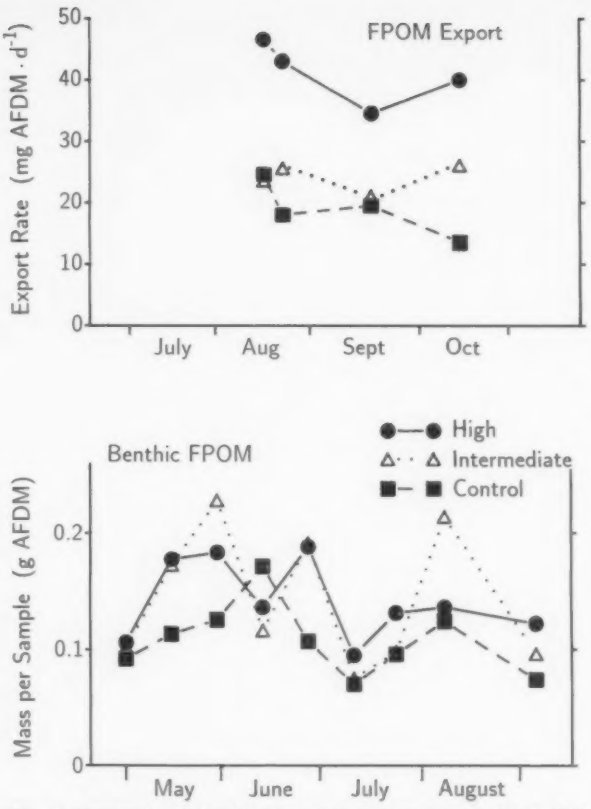

FIG. 2. Exported and benthic fine-particulate organic matter FPOM (ash-free dry mass, AFDM) in the size range 0.471–1.0 mm. Upper panel: daily export rate of FPOM in this size fraction; lower panel: FPOM of the same size fraction from benthic samples.

miscellaneous Trichoptera (mostly early instar lepidostomatids and limnephilids), and Copepoda and all had higher densities in channels receiving high input rates of leaves.

The effects of detrital input manipulations on benthic densities of individual taxa of nonshredders were not significant in parametric analyses, so the ranks of the least square means for density of each taxon were compared among treatments. The densities in channels with high detrital input were greater than in control channels for 30 of 36 taxa (sign test, $P < 0.001$) and greater than the intermediate treatment for 27 of 35 taxa (including one tie, sign test, $P < 0.005$). Twenty-four of 36 comparisons were higher in the channels with intermediate detrital input than the control channels, but this difference was not significant (sign test, $P > 0.05$).

Density trends within trophic levels were also compared by rank of the least square means. Predator taxa were more dense in the high-detritus input channels versus the intermediate level channels for 11 of 13 taxa (sign test, $P < 0.03$) and higher than "natural" densities for 10 of 13 taxa (sign test, $0.09 < P < 0.1$). Seven of 13 taxa had higher densities in the channels with intermediate detrital addition rates. The combined predator density was higher with increased detrital input (Fig. 3) but not significantly so (ANOVA, $F_{2,3} = 1.69$, $P > 0.3$).

The rankings of collector densities among treatments were significantly different in the order high > intermediate > control. Fifteen of 19 taxa were more dense in high versus inter-

TABLE 1. Results of tests of treatment effects on benthic densities of invertebrate taxa for the period 15 May to 4 September 1986. Groupings of taxa into trophic groups follows that of Merritt and Cummins (1984) and Pennak (1978). Rank numbers are 3 = high detritus input rate, 2 = intermediate rate, 1 = control. Critical α for statistical significance is 0.0014 after application of the Bonferroni correction.

Taxon	$F_{2,3}$	P	Rank
Predators			
Perlidae (Plecoptera)	3.21	0.18	3>1>2
Perlodidae (Plecoptera)	3.08	0.19	3>1>2
Chloroperlidae (Plecoptera)	0.47	0.66	1>3>2
Drunella spinifera (Ephemeroptera)	1.48	0.36	2>1>3
Rhyacophila spp. (Trichoptera)	1.29	0.39	3>2>1
Polycentropus + *Parapsyche* (Trichoptera)	0.17	0.85	1>3>2
Tanypodinae (Diptera)	1.95	0.29	3>2>1
Oreogeton sp. (Diptera)	2.86	0.21	3>2>1
Ceratopogonidae (Diptera)	2.36	0.24	3>2>1
Hexatoma sp. (Diptera)	0.91	0.49	3>2>1
Dicranota sp. (Diptera)	3.33	0.18	3>1>2
Acari	2.32	0.25	3>1>2
Turbellaria (Platyhelminthes)	0.51	0.65	2>3>1
Collectors			
Baetis spp. (Ephemeroptera)	1.05	0.45	3>2>1
Paraleptophlebia debilis (Ephemeroptera)	0.62	0.60	3>2>1
P. temporalis (Ephemeroptera)	0.43	0.69	2>3>1
Ameletus sp. (Ephemeroptera)	0.26	0.79	3>1>2
Serratella tibialis (Ephemeroptera)	2.56	0.22	3>2>1
Epeorus sp. (Ephemeroptera)	2.09	0.27	2>3>1
Tanytarsini (Diptera)	2.36	0.24	3>2>1
Chironomini (Diptera)	24.39	0.02	3>2>1
Corynoneura spp. (Diptera)	4.55	0.12	3>2>1
Miscellaneous Orthocladiinae (Diptera)	7.90	0.07	3>2>1
Simuliidae (Diptera)	9.69	0.05	3>2>1
Wormaldia anilla (Trichoptera)	1.66	0.33	3>2>1
Ecclisomyia conspersa (Trichoptera)	0.04	0.96	3>1>2
Miscellaneous Trichoptera	8.90	0.05	3>1>2
Elmidae (Coleoptera)	1.87	0.30	3>2>1
Oligochaeta	3.44	0.17	3>1>2
Ostracoda	0.92	0.49	2>1>3
Copepoda	10.73	0.04	3>2>1
Sphaeriidae (Pelecypoda)	5.04	0.11	2>1>3
Grazers			
Hydroptilidae (Trichoptera)	4.58	0.12	2>3>1
Cinygmula sp. (Ephemeroptera)	0.41	0.69	1>2>3
Cinygma sp. (Ephemeroptera)	1.13	0.43	3>1>2
Ironodes sp. (Ephemeroptera)	3.53	0.16	3>2>1

mediate and intermediate versus control channels (sign test, $P < 0.02$). High-detritus channels had 17 of 19 taxa with higher densities than controls (sign test, $P < 0.001$). To illustrate the overall effects of the three treatments, the total numbers per sample for all collectors (including filter feeders) were calculated (Fig. 3). There was a significant treatment effect (ANOVA, $F_{2,3} = 211$, $P < 0.001$), with all three treatments significantly different from each other (Tukey's test, $P < 0.05$) in the order high > intermediate > control. Because of omnivory of nymphs of *Baetis*, *Epeorus*, and *Paraleptophlebia*, the data for collector densities were reanalyzed excluding these taxa; again, the treatment effect was significant (ANOVA, $F_{2,3} = 507$, $P = 0.0002$), with all treatments significantly different (Tukey's test). Filter feeders are uncommon in Mayfly Creek and the channels, but when the densities of simuliids and *Wormaldia anilla* were combined, there was a statistically significant difference in densities (ANOVA, $F_{2,3} = 127$, $P = 0.0013$), with significant differences between all three treatments (high > intermediate > control, Tukey's test).

The four taxa listed as grazers showed no trend in density ranks related to treatments (Table 1). There was no significant difference in the combined densities of grazers due to treatment (Fig. 3, $F_{2,3} = 1.98$, $P > 0.25$). When densities of *Baetis* and *Epeorus* were added to the other grazers, there was still no significant difference (ANOVA, $F_{2,3} = 1.05$, $P > 0.45$).

We tested for treatment effects on numbers of taxa per sample to determine whether detrital manipulations affected taxon richness (Fig. 4). The numbers of taxa per sample included shredders and rare taxa not listed in Table 1. There was an increase in richness over the summer with hatching of eggs of many species. Although the number of taxa per sample was slightly higher with higher detrital loading, ranging from 21.3 taxa in the control channels to 24.1 under high detrital input, there was no statistically significant effect of treatment (ANOVA, $F_{2,3} = 1.69$, $P > 0.3$).

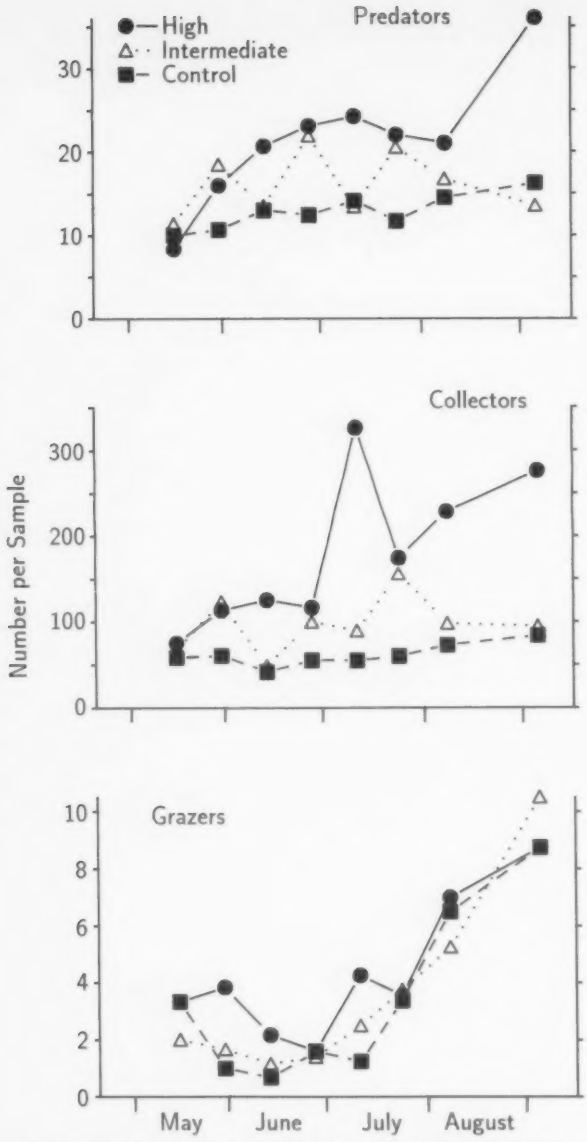

FIG. 3. Benthic densities of total collectors, predators, and grazers in experimental stream channels with whole-leaf detritus additions. Each point represents the mean of five samples from each of the two replicate channels. Area of each sample was 402 cm^2.

Emigration and Immigration

The numbers of emigrants from and immigrants to each channel were compared with repeated measures ANOVA for 29 taxa for which there were sufficient individuals (Table 2). There were no significant differences due to treatment in either emigration or immigration rates. To test for trends of emigration and immigration rates for each treatment for all taxa, we used ranks of the rates by treatment. There were no significant trends in either emigration or immigration rates in favour of any treatment for all taxa. The only trend in the rankings was that the emigration rate of predators was higher from the control channels than channels receiving intermediate amounts of detritus (9 of 10 taxa, sign test, $P < 0.03$).

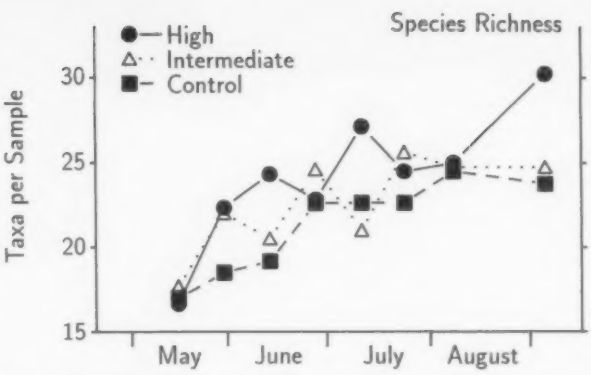

FIG. 4. Species richness measured as taxa per sample for the three detritus input rate treatments. Each point represents the mean of the two replicate channels (based on the means of all samples on that date in each channel). Values include shredders and some rare taxa not listed in Table 1.

The numbers of emigrants and net colonization (immigrants minus emigrants) in each trophic category were also analyzed and there were no significant effects due to treatment (ANOVA, all with $P > 0.25$). The net rates of colonization using the least squared means for collectors (including or excluding *Baetis*, *Epeorus*, *Paraleptophlebia*, and the filterers) were lowest for the high leaf input treatment. Filterers had a negative net rate of colonization for all channels, with the highest loss rate, although not statistically significant, from the intermediate detrital addition channels. The grazers had a higher net rate of colonization to the channels receiving high rates of detrital input, but this difference was not significant ($P > 0.05$).

Adults

For a few taxa, sufficient numbers of adults were collected in emergence cages to test for treatment effects on individual dry mass, head width, and wing length. The data on all three measurements of *Baetis* spp. ($n = 430$), *Cinygmula* sp. ($n = 118$), *Cinygma* sp. ($n = 35$), *Ameletus* sp. ($n = 54$), *Sweltsa fraterna* ($n = 30$), and *S. occidens* ($n = 22$) were fitted to an ANCOVA with treatment, sex, and stream-within-treatment as main effects, and date as a covariate, after which the treatment effect was tested using stream-within-treatment as the error term. In most cases, there were significant effects of sex and date on dry mass, head width, and wing length ($P < 0.05$). None of the three measures of size differed significantly ($P > 0.05$) among treatments for any of the six taxa.

Discussion

The results of our detritus addition experiment indicate that even on a moderately small spatial scale, increased coarse-detritus additions can lead to increased densities of collectors, presumably through the activities of shredders. A central assumption of some current views of stream ecosystem function is that the FPOM available to collectors is derived from the feeding activities of detritivores (Cummins 1974; Vannote et al. 1980). It has even been argued that the major role of detritivores in lotic ecosystems is the conversion of coarse detritus to FPOM (Webster 1983). Indeed, Wallace et al. (1982) have shown that CPOM consumers can generate a large proportion of the suspended FPOM as a result of their feeding activities. However,

TABLE 2. Results of tests of treatment effects on emigration or immigration rates of invertebrate taxa. Groupings of taxa into trophic groups follows that of Merritt and Cummins (1984) and Pennak (1978). Ranks are as described for Table 1. Critical α for statistical significance is 0.0017 after application of the Bonferroni correction.

Taxon	Emigration			Immigration		
	$F_{2,3}$	P	Rank	$F_{2,3}$	P	Rank
Predators						
Perlidae (Plecoptera)	1.28	0.40	3>1>2	0.78	0.54	3>1>2
Perlodidae (Plecoptera)	2.00	0.28	3>1>2	0.00	0.99	1>2>3
Chloroperlidae (Plecoptera)	0.01	0.99	3>1>2	0.29	0.77	1>3>2
Rhyacophila (Trichoptera)	0.99	0.47	1>3>2	0.97	0.47	3>2>1
Tanypodinae (Diptera)	1.63	0.33	1>2>3	1.43	0.37	3>1>2
Hexatoma sp. (Diptera)	2.66	0.22	3=2>1	38.50	0.01	2>3>1
Dicranota sp. (Diptera)	5.63	0.10	3>1>2	0.05	0.97	1=2>3
Ceratopogonidae (Diptera)	2.94	0.20	3>1>2	4.11	0.14	3>2>1
Turbellaria (Platyhelminthes)	0.14	0.88	1>2>3	0.66	0.58	2>1>3
Acari	1.12	0.43	1>2>3	0.55	0.62	2>3>1
Collectors						
Baetis spp. (Ephemeroptera)	0.20	0.83	3>2>1	11.66	0.04	3>2>1
Paraleptophlebia debilis (Ephemeroptera)	1.21	0.41	3>1>2	16.67	0.02	1>2>3
P. temporalis (Ephemeroptera)	0.40	0.70	1>3>2	0.20	0.83	1>3>2
Ameletus sp. (Ephemeroptera)	0.82	0.52	1>3>2	0.05	0.95	2>3>1
Serratella tibialis (Ephemeroptera)	14.37	0.03	1>2>3	2.37	0.24	1>2>3
Epeorus sp. (Ephemeroptera)	1.25	0.40	3>1>2	0.75	0.54	3>1>2
Tanytarsini (Diptera)	0.45	0.67	2>1>3	0.32	0.75	3>2>1
Chironomini (Diptera)	1.80	0.31	3>2>1	0.44	0.68	1>3>2
Corynonuera spp. (Diptera)	0.83	0.52	3>2>1	0.30	0.76	3>1>2
Miscellaneous Orthocladiinae (Diptera)	1.56	0.34	3>2>1	1.09	0.44	3>2>1
Simuliidae (Diptera)	0.82	0.52	2>1>3	0.01	0.99	3>1>2
Elmidae (Coleoptera)	0.62	0.60	1>2>3	0.21	0.82	1>2>3
Wormaldia anilla (Trichoptera)	1.45	0.36	1=2>3	0.69	0.57	1>3>2
Miscellaneous Trichoptera	1.39	0.37	1>2>3	0.01	0.99	3>2>1
Oligochaeta	0.16	0.86	2>1>3	0.63	0.59	3>2>1
Crustacea	1.00	0.46	2>3>1	1.81	0.30	3>1>2
Grazers						
Ironodes sp. (Ephemeroptera)	4.96	0.11	1>3>2	8.97	0.05	1>3>2
Cinygma sp. (Ephemeroptera)	1.30	0.39	2>1>3	11.56	0.04	3>1>2
Cinygmula sp. (Ephemeroptera)	2.88	0.20	3>1>2	0.30	0.76	1>2=3

aside from laboratory demonstrations where the only source of FPOM was from detritivores (Short and Maslin 1977), there have been no field tests of the assumption that this source of FPOM has a positive effect on collectors (Winterbourn et al. 1981). Calculations of the quantity of fine particles produced by detritivore feeding activities have suggested that this is a primary source of FPOM. However, studies of food value of FPOM have shown shredder faeces to be of higher quality than average FPOM from natural streams (Short and Maslin 1977; Ward and Cummins 1979; Mattingly 1987). Naiman (1983) has shown that a large fraction of suspended FPOM is composed of low-quality, lignified particles.

Collector densities (as a composite group) were positively affected by manipulations of whole-leaf detritus, and this was also true of the subgroups filterers and gatherers (sensu Cummins 1973). The densities of most collector taxa were higher under detritus addition. The increased densities for each taxon were not significant and neither were the effects on rates of emigration, or on size of adult *Baetis* spp. or *Ameletus* sp. While there was a large and significant increase in the densities of collectors as a trophic category, coarse-detritus additions resulted in only moderate increases of most individual taxa. The absence of significant differences in the rates of emigration and immigration for collectors suggests that the density differences were due to increased survival of larvae in the channels with higher rates of leaf addition. In fact the colonization rates of gathering collectors were lowest for the high-input channels so that enhanced survival seems the best explanation. The negative net colonization by filterers probably represents the decrease in total numbers of individuals that can be supported as biomass increases due to growth. Again, since the emigration and immigration rates did not differ significantly, the higher densities must be due to higher survival or carrying capacity when coarse detritus was enhanced.

There are alternative explanations for the increases in collector densities when whole-leaf detritus was added. One possibility is that some of these taxa fed directly upon CPOM. This explanation is unlikely for most taxa such as blackflies (Simuliidae), *Wormaldia anilla* (Trichoptera), Copepoda, and Chironomini (Chironomidae). Species such as Simuliidae and Chironomini were seldom found on leaf packs, but may have fed upon flocs formed from the dissolved organic carbon leached from the leaves; this would be a direct effect. The proportion of leaf mass loss to leaching was only about 15% and the dissolved organic carbon would probably not form flocs within the short length of the channels. Another alternative explanation is that alteration of the microhabitat by the addition of coarse detritus may have influenced densities. Evidence from

an experiment comparing colonization of alder and polyester leaf packers suggests that FPOM concentration, and not microhabitat alone, accounted for the distribution of most of the collector taxa (Richardson 1989).

The export of organic particles of size 0.471–1.0 mm in diameter was approximately doubled when leaf input rate was increased 40 times whereas the concentrations of benthic organic matter in the same size fraction did not differ significantly among treatments. The increased densities of the filterers suggest that the increased supply of FPOM was used by these taxa. However, the absence of significant differences of benthic FPOM between treatments was surprising. The consumption of CPOM by detritivores should have resulted in higher rates of accumulation of FPOM with increased leaf additions, in part by the increased retention by leaves. The lack of such accumulations in the channels may have been caused by consumption by collectors, or by the activity of increased densities of macroinvertebrates causing erosion of fine particles and loss to export. Our data do not allow us to define the pathways of FPOM processes. However, one hypothesis would be that the excess FPOM produced with high leaf input rates went directly to the support of increased collector biomass.

The density of predators did not increase significantly under higher leaf loading. In light of increased densities of potential prey due to detritus addition (collectors and shredders, Richardson 1991), one might predict a large aggregative response on the part of the predators, but this did not occur. Most of the difference in total predator numbers among treatments was a result of increased density of larvae of the midge subfamily Tanypodinae. The absence of a distinct responce by most predator taxa may have been attributable to two possibilities. First, many predatory stream invertebrates are known to exhibit strong interference interactions among themselves (Hildrew and Townsend 1980; Walde and Davies 1984; Peckarsky and Penton 1985). Interference among predators may prevent local increases in densities in spite of increased prey abundance. Second, relatively low densities of predators in Mayfly Creek (relative to detritivores and collectors) may have limited the number of potential colonists to the channels. A potential implication of this result is that if predators are incapable of showing an aggregative or functional response (the latter which we could not measure) to increased prey densities, then predators may not be capable of regulating prey populations.

Grazers were represented by only a few taxa in this oligotrophic montane stream. There was no evidence for differences in densities of grazers related to treatment. The only likely mechanisms that might have produced a response among grazers were (i) altered microhabitat, (ii) fertilization by nutrients leached from CPOM, or (iii) reduced predation pressure. The absence of an effect of detritus manipulations on grazers further suggests that alteration of microhabitat was not influential in producing the observed patterns of density.

Variations in both food quality and quantity seem to influence consumer abundance. Several authors have shown that the average quality of FPOM, as expressed by collector growth rates, from streams is lower than that of ground-up leaf detritus or shredder faeces (Short and Maslin 1977; Ward and Cummins 1979; Mattingly 1987). Positive correlations between seston quality and density of fine-particle collectors have been observed by several authors (Georgian and Wallace 1981; Petersen 1987; Valett and Stanford 1987). Indeed, the river continuum concept states that collectors depend on FPOM export, which implies that collectors are food limited (Vannote et al. 1980). The timing of our experiment increased our ability to detect changes in collector and FPOM levels, since the background concentrations during summer are typically lower than during autumn and winter when higher CPOM inputs and more frequent spates increase FPOM concentrations. If our interpretation that the increase in collector densities was due to enhanced food supply as a result of increased FPOM derived from shredder feeding is correct, then this would mean that population densities of collectors are sometimes food limited. Low rates of CPOM input to streams like Mayfly Creek at some times of the year, e.g. summer, may result in constraints on population densities for certain collector taxa, as has been shown for shredders (Richardson 1991).

Indirect effects among community members may be subtle and take several generations to be measurable (Bender et al. 1984; Davidson et al. 1984; Carpenter 1988). A long-term experiment in these stream channels would have been confounded by the reduction in the natural regime of hydrologic disturbance from winter and spring freshets. Nevertheless, the effects measured in our experiment indicate a rapid response of density, presumably as a function of increased carrying capacity. The increase in the ability to support higher densities of collectors should translate to higher population densities in the longer term. Most taxa were unable to undergo numerical responses during the course of the experiment, since most have univoltine life cycles. However, the increases in densities, which appear to come about due to increased survival, would be expected to maintain higher population densities of collectors. In spite of the limited power of the experiment, i.e. only two replicates per treatment (Toft and Shea 1983; Rotenberry and Wiens 1985), some indirect effects were apparent as a consequence of whole-leaf detritus additions.

Increased densities of collectors with increased CPOM input supports the hypothesis that populations of FPOM feeders were facilitated by the manipulation. The effect of the manipulation was to increase the survival rate of collectors at higher rates of litter input. The actual pathway through which the positive effects on collectors were manifest could not be determined in our experiment, but increased FPOM production as a result of the feeding activities of shredders seems most likely. That the response was detectable within 2 mo, on the spatial scale of the experimental stream channels, demonstrates the intensity and potential importance of this interaction.

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Evaluation of Escape Modifications in Traps for Prawn, *Pandalus platyceros*

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Experimental fishing was done in 1986 to evaluate variables considered important in developing escape modifications for the prawn, *Pandalus platyceros*, trap fishery in British Columbia. Three major trap categories were used: flexible nylon mesh, rigid wire mesh, and solid sided. The efficacy of escape modifications depended upon the size of openings, the type of construction material, the placement of the modification on the trap, and soak time. The 44-mm web and wire material used for modifications allowed for escapement of prawns well above the 30.0-mm carapace length legal size limit. The rigid wire mesh used in escape modifications retained smaller prawns than did similar-sized flexible nylon mesh. In partially modified traps, escape material on the side/bottom combination was more effective for escapement than when just on the bottom or in the tunnels of the trap. Soak time was important in some traps which had escape material in ineffective locations. In these cases, longer soak times allowed the small prawns time to find their way out of the traps.

Une pêche expérimentale à la crevette tachée, *Pandalus platyceros*, a été effectuée en 1986 pour évaluer certains paramètres considérés importants pour favoriser l'échappée des crevettes de taille non réglementaires des casiers utilisés en Colombie-Britannique. Trois catégories importantes de casiers ont été considérées : ceux en filet de nylon souple, en grillage métallique rigide et à parois pleines. L'efficacité des modifications apportées aux casiers était fonction de la taille des ouvertures, du type de matériel utilisé, de l'endroit où les modifications ont été apportées et de la durée du mouillage. Le tissu et le grillage de maillage de 44 mm utilisés pour les modifications laissaient passer les crevettes dont la carapace avait une longueur bien supérieure à la limite permise par le règlement, soit 30,0 mm. Le grillage métallique rigide utilisé retenait des crevettes de plus petite taille que celles retenues par le filet de nylon souple de maillage de même dimension. Dans le cas des casiers partiellement modifiés, les modifications étaient plus efficaces quand elles étaient apportées à la fois sur les côtés et le fond plutôt que seulement sur le fond ou au niveau des goulets. Dans le cas des trappes dont les modifications se sont montrées inefficaces en raison de leur localisation, la durée du mouillage était un paramètre important : en effet, avec un mouillage de plus longue durée, les petites crevettes avaient plus de temps pour trouver un endroit par où s'échapper.

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In all fisheries, if a factor causes the size and age composition of the catch to be different from that of the actual population, it is said to be affecting the selectivity of that fishery (Pope 1975). The selectivity of trap fisheries is often managed to control the size and age structure of catches. This is achieved by (1) controlling the time and area of a fishery to coincide with seasonal differences in population structure (Thomas 1958; Morgan 1974) or protecting areas with concentrations of brood females or nursery stock (Miller 1976) and (2) requiring escape modifications in fishing gear, such as lath spacing in lobster traps (Wilder 1945, 1948) or escape rings in crab traps (Miller 1976).

In the past decade, trap fishing effort for prawns, *Pandalus platyceros*, in British Columbia has increased fivefold to 241 vessels and 100 000 traps in 1985 (Boutillier and Sloan 1987). Prior to 1979, this widespread, yet discretely distributed inshore fishery was unregulated. Concerns about growth overfishing led Boutillier (1984, 1985a) to recommend a minimun size limit of 30.0 mm carapace length (CL) for *P. platyceros*. However, industry and management stressed that reliance on a size limit alone would be unenforceable and they suggested modification of fishing gear to provide appropriate escapement.

Developing escape modifications for the fishing gear in this fishery is complicated because of the great diversity of trap designs used. Over 30 prawn trap designs have been identified from commercial fishery assessment data (Boutillier 1985b). However, all designs fall into three categories depending on the trap covering: (1) flexible nylon mesh, (2) wire mesh, and (3) solid material, e.g. wood.

This study was designed to determine the factors that are important in the development of viable and easily installed escape modifications for each of the above trap categories. Industry was solicited for suggestions as to the location and extent of implementable escape modifications for each trap category. These modifications were then tested against unmodified control traps to determine their efficacy in providing

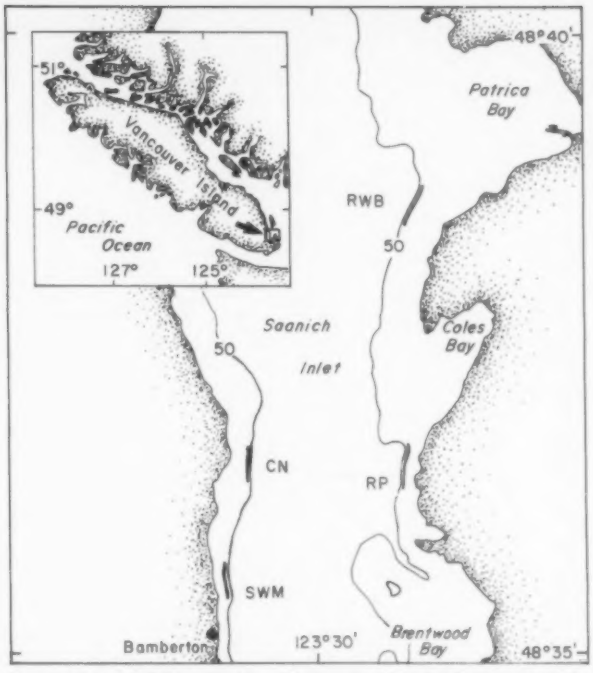

FIG. 1. Saanich Inlet, southern Vancouver Island, showing the 50-fathom (92.3-m) isobath and fishing localities for the conical nesting (CN), round "Pardiac" (RP), square wire mesh (SWM), and rectangular wooden box (RWB) traps.

escapement of prawns below, and retention of those above, the minimum size limit.

Materials and Methods

Four experiments were conducted in Saanich Inlet (Fig. 1) during May 1986. This inlet, a productive prawn area, had been closed to commercial prawn fishing for the previous two seasons and remained closed during the experiments. Two experiments were conducted using different types of traps (conical and round) covered with flexible nylon mesh (Fig. 2A "CONE," 2B "ROUND"), a third with rigid wire mesh traps (Fig. 2C "WIRE"), and the fourth with wooden solid-sided traps (Fig. 2D "WOOD"). Each experiment was conducted at separate sites which contained fishable concentrations of sublegal- and legal-size prawns as determined from a series of prestudy sets in the inlet.

Specifications for each of the control and escape-modified trap variations are listed in Table 1. All modified traps used material which met the Washington State *P. platyceros* fishery mesh regulations (Anonymous 1986).

Seven traps of each variation were used in each set. Sets were repeated five times each at 24- and 48-h soaks, which are standard soak times used throughout the industry (Boutillier and Sloan 1987). Traps were set in random sequence, 18 m apart, along a ground line deployed at 75- to 90-m depth at each site as shown in Fig. 1. Each trap was baited with a punctured 100-g can of sardines packed in edible oil. Baits were used only once. Captured prawns were counted, their carapace length measured (posterior orbital rim to median dorsal carapace edge (Rasmussen 1953; Butler 1980)), and retained.

Mean size of captured prawns was calculated for each trap variation and soak time combination. A Kolmogorov–Smirnov (KS) test was used to compare the difference between the size distribution of animals retained after 24- and 48-h soaks for each trap variation. Size compositions and catch per unit of effort (CPUE) from unmodified traps (CONE-Control, ROUND-Control, WIRE-Control, and WOOD-Control) were used for comparison with appropriate escape modified traps to produce the prawn size selection ogives (after Pope 1975) (i.e. the plot of the proportion retained against carapace length). In calculating a quantitative expression to fit the selection ogive, the proportion-retained data were transformed (after Pope 1975) to their equivalent normal deviate using a table of probits (Fisher and Yates 1963, table IX). A linear regression was performed on the probits of the proportion retained against the carapace lengths. The 50% retention carapace length and the selection range (i.e. the range of lengths between the 25 and 75% retention lengths on the selection curve (Pope 1975)) were calculated for each escape-modified trap variation by soak time.

In each time of the four experiments, the data were analyzed to determine if trap variations had significant differences in catch rates, where catch rate was broken into numbers in prawns retained $\geq$30.0 mm CL (legal) and $<$30.0 mm CL (sublegal).

The data analyzed were catch of each trap hauled. The actual number of replicates used in the analysis for any single trap/soak variation was 27–35. The unbalanced number of replicates was due to data missing from lost and damaged traps. The homoscedasticity of the original data was examined using Levene's test for equal variance (Dixon 1985) to determine whether the data met assumptions required for an analysis of variance (ANOVA). The variances of data from each experiment were found to be heteroscedastic, so the data were transformed using a square root transformation. A square root transformation of the data was selected as suggested by Zar (1984) for data consisting of counts of randomly occurring objects or events. It is also the transformation suggested from a Box and Cox transformation estimation procedure (Dixon 1985) where the logarithm of the cell standard deviation was regressed on the logarithm of the cell mean. The dependent variable is then raised to the power $1-b$ where b is the regression coefficient. An ANOVA was then conducted on the transformed legal and sublegal catch data in each of the four experiments. A nonparametric two-factor ANOVA, an extension of the Kruskal–Wallis test (Zar 1984), was also conducted. The results of the two tests were equivalent, so only the parametric ANOVA results will be presented. An a posteriori Tukey multiple comparison test was conducted on the main factors and interactions to determine where significant ($P < 0.05$) differences occurred.

Results

Size Composition

All escape modifications were successful in reducing to varying degrees the catch of sublegal prawns. Soak time variations often led to significant differences in the size composition of the animals retained.

CONE traps

On average, for both soak times, $\approx$29% of the catch retained in Control traps was composed of animals below the minimum size limit. In the escape-modified traps the percentage of sublegal catch decreased to $\approx$1 and $\approx$12% for the Total and Bottom traps, respectively (Table 2). The mean carapace length of

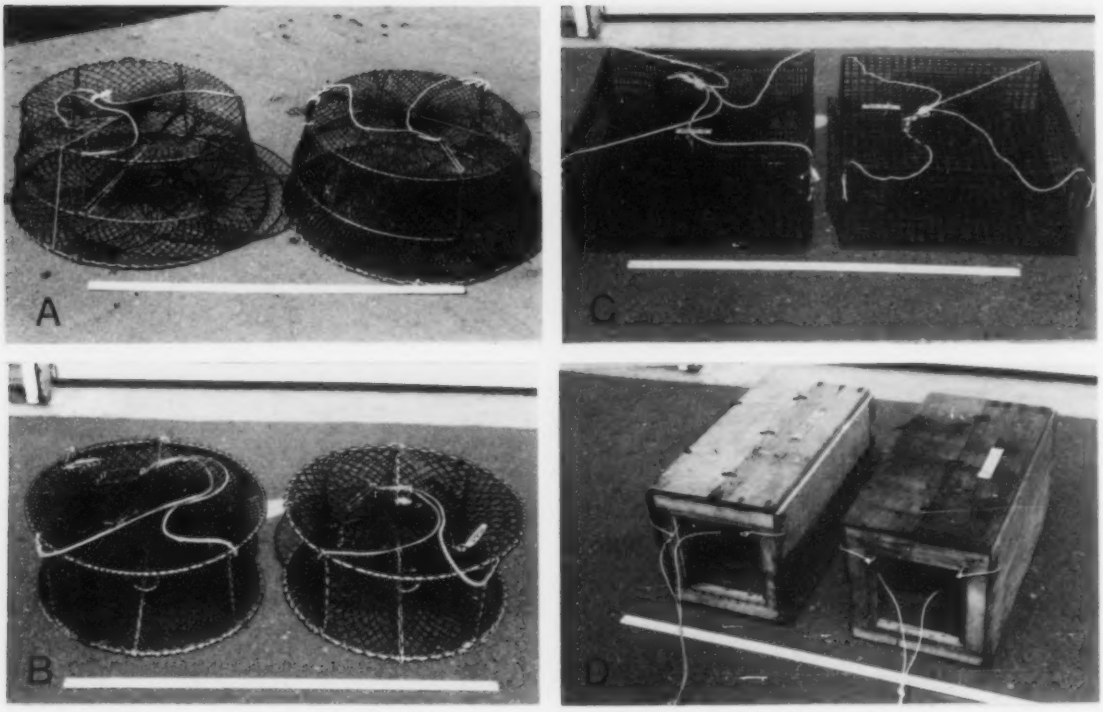

FIG. 2. Trap variations. (A) Conical nesting: CONE-Total on left and CONE-Control on right; (B) round "Pardiac": ROUND-Control on left and ROUND-Total on right; (C) square wire mesh: WIRE-Control on left and WIRE-Total on right; (D) rectangular wooden box: WOOD-Panel on left and WOOD-Control on right. Scale bar = 1.0 m.

prawns caught was larger (0.5 – 2.0 mm) in the longer 48-h soaks in all three variations of CONE traps (Table 3) as compared with 24-h soaks. The KS test of the size frequency distributions showed significant differences between the 24- and 48-h soak times for the Control and Bottom modified traps.

ROUND traps

The control variation showed the highest percentage retention of CL < 30.0 mm prawns (≈21%), while the escape-modified traps showed average percentages of sublegal catches of ≈1, ≈6, ≈3, and ≈3% for the Total, Panel, Bottom & Side, and Pursed & Side modified traps, respectively. As in the CONE traps, 48-h soaks resulted in larger (0.1 – 1.1 mm) mean prawn sizes compared with 24-h soaks (Table 3) for all five ROUND trap variations. A KS test of the 24- and 48-h distributions found a significant difference in the Panel and Bottom & Side trap variations.

WIRE traps

Of the three variations of square wire mesh traps, the Control traps retained the highest proportion of sublegal prawns (≈49%). This was reduced to ≈1 and ≈20% for the Total and Bottom traps, respectively (Table 2). Unlike the other trap types, increasing soak time to 48 h reduced (0.1 – 0.8 mm) the mean size of captured prawns in the Control and Bottom traps (Table 3). A KS test found a significant difference between the 24- and 48-h size frequency distribution of the Control traps.

WOOD traps

For Control traps, ≈39% of the catch was composed of prawns with CL < 30.0 mm, while the catch retention patterns of same-sized prawns for the escape-modified Tunnel, Slot, Panel, and Bottom traps were ≈4, ≈7, ≈6, and ≈4%, respectively (Table 2). For all five trap variations, the mean size of retained prawns was larger (0.9 – 2.0 mm) for the 48-h soaks than for the 24-h soaks (Table 3). A KS test comparing the 24- and 48-h size frequency distributions found significant differences in all trap variations except the Panel traps.

Selection Ogives

With the exception of CONE-Bottom (24-h soak) and WIRE-Bottom (24- and 48-h soak) modified traps, the 50% selection ogives for the escape-modified traps were above the 30.0-mm legal size limit (Table 4).

CONE traps

Of the escape modified traps, the 50% retention sizes were smaller for Bottom traps then for Total traps, at both soaks. The sharpness of the selection, or selection range (Pope 1975), is finer for Total traps then Bottom traps (Table 4).

ROUND traps

The 50% retention sizes (Table 4) show the Panel traps retaining a consistently smaller prawn then the other ROUND escape-modified traps. Of the escape-modified traps, the Total traps show the tightest selection range.

WIRE traps

In a comparison of the Bottom and Total traps, the Bottom traps retained a smaller prawn. The selection ranges, however, were tighter for the Total traps (Table 3).

WOOD traps

For the escape-modified traps, the 50% retention size were the smallest in the Tunnel traps followed by the Slot, Bottom,

TABLE 1. Characteristics of variations of the four different traps used. The CONE and ROUND traps had metal frames covered by nylon mesh, the WIRE mesh were rigid plastic-covered mesh, and the WOOD traps were constructed of wood slabs with a tunnel at each end lined with nylon mesh. N.A. = not applicable.

		Frame characteristics			Trap coverage characteristics		
		Dimensions (cm)					
Trap	No. of variations	Top × bottom × side	Volume (L)	Variation	Mesh size (mm)[a]	% coverage	Location
CONE	3	63[b] × 76[b] × 30	110	Control	29	100	
				Total	44	100	
				Bottom	29	64	
					44	36	Bottom only
ROUND	5	60[b] × 60[b] × 24	69	Control	29	100	
				Total	44	100	
				Panel	29	89	
					44	11	Panel on side
				Bottom & Side	29	61	
					44	39	Bottom (stretched taut) and side panel
				Pursed & Side	29	61	
					44	39	Bottom (pursed) and side panel
WIRE	3	61(*l*) × 61 (*w*) × 28 (*h*)	104	Control	12 × 22	100	
				Total	22 × 22	100	
				Bottom	12 × 22	74	
					22 × 22	26	Bottom only
WOOD	5	61 (*l*) × 33 (*w*) × 33 (*h*)	66	Control	N.A.	100	
				Tunnel	44	11	Tunnel linings
				Slot	N.A.	N.A.	Four (16 × 160 mm) slots
				Panel	44	22	Panel on bottom half of each of two opposing sides
				Bottom	44	22	Bottom only

[a]Black notted nylon stretched mesh web measured knot to knot or measured sides of rigid wire mesh.
[b]Diameter.

TABLE 2. Number of traps hauled, mean numbers of prawns per trap, and percentage of catch of prawns, CL < 30.0 mm, for each trap type and modification by soak time.

	24 h			48 h		
Trap	Traps hauled	$\bar{x}$ catch/trap	% sublegals	Traps hauled	$\bar{x}$ catch/trap	% sublegals
CONE						
Control	34	78.0	35.7	34	70.6	21.4
Total	35	24.9	0.6	35	25.8	1.2
Bottom	35	49.0	15.0	35	50.1	8.3
ROUND						
Control	35	20.2	23.9	34	19.3	18.3
Total	35	11.8	1.4	35	17.1	0.5
Panel	35	10.1	7.9	35	14.9	3.5
Bottom & Side	35	8.5	4.0	35	10.5	2.2
Pursed & Side	34	6.6	3.1	35	12.3	3.2
WIRE						
Control	34	97.7	43.3	28	92.4	54.1
Total	34	41.9	0.6	28	30.0	0.8
Bottom	35	62.1	18.3	28	55.9	20.7
WOOD						
Control	35	83.0	44.8	27	66.6	33.9
Tunnel	35	37.1	5.5	28	36.5	3.0
Slot	34	29.2	12.8	28	28.0	0.8
Panel	35	23.0	6.0	28	26.5	5.5
Bottom	35	28.1	5.1	28	21.2	3.2

TABLE 3. Mean sizes and KS test results of prawns caught according to trap characteristics by soak time. NS = not significant; *$\bar{x}$ 48 h > $\bar{x}$ 24 h ($P < 0.05$); **$\bar{x}$ 24 h > $\bar{x}$ 48 h ($P < 0.05$).

Trap	Modification	Mean prawn size (mm) 24 h	48 h	KS test two-sided P
CONE	Control	31.5	33.5	0.000*
	Total	37.0	37.5	0.427 NS
	Bottom	34.3	35.6	0.029*
ROUND	Control	33.1	34.1	0.153 NS
	Total	37.7	38.3	0.126 NS
	Panel	36.1	36.9	0.011*
	Bottom & Side	36.8	37.9	0.020*
	Pursed & Side	37.5	37.6	0.752 NS
WIRE	Control	30.9	30.1	1.99×10^{-4}**
	Total	36.9	36.9	0.153 NS
	Bottom	33.7	33.6	0.162 NS
WOOD	Control	30.9	32.9	0.000*
	Tunnel	36.9	38.9	2.38×10^{-7}*
	Slot	37.1	38.0	0.012*
	Panel	37.3	38.2	0.220 NS
	Bottom	37.5	38.4	0.010*

TABLE 4. Twenty-five, 50, and 75% retention (CL) ogives and selection ranges of prawns according to trap characteristics and soak time.

Trap	Mesh variation	Soak (h)	Ogive (mm) 25%	50%	75%	Selection range
CONE	Total	24	32.8	34.8	36.8	4.0
		48	33.9	36.2	38.5	4.6
	Bottom	24	25.3	29.3	33.2	7.9
		48	28.8	31.3	33.7	4.9
ROUND	Total	24	32.6	34.7	36.8	4.2
		48	32.7	34.7	36.7	4.0
	Panel	24	29.2	33.5	37.7	8.5
		48	30.7	32.7	34.7	4.0
	Bottom & Side	24	30.6	34.6	38.6	8.0
		48	33.5	35.2	36.9	3.4
	Pursed & Side	24	34.1	36.6	39.1	5.0
		48	31.9	34.3	36.8	4.9
WIRE	Total	24	32.5	33.9	35.3	2.8
		48	33.0	34.7	36.4	3.4
	Bottom	24	25.9	28.5	31.2	5.3
		48	24.4	27.9	31.4	7.0
WOOD	Tunnel	24	30.9	33.7	36.5	5.6
		48	32.1	34.9	37.7	5.6
	Slot	24	31.4	34.3	37.3	5.9
		48	32.5	35.4	38.4	5.9
	Panel	24	33.5	36.8	40.2	6.7
		48	35.1	37.4	39.4	4.3
	Bottom	24	32.5	35.6	38.7	6.2
		48	34.1	36.4	38.8	4.7

and Panel traps. The selection ranges were consistent between the 24- and 48-h soaks for the Tunnel and Slot modified traps but tended to decrease for the Panel and Bottom traps with the longer soak time (Table 4).

Catch Rates

In each of the four experiments, both the CPUE's for legal and sublegal prawns were affected by either one or both of the main effects, i.e. trap modification or soak time and/or their interaction.

CONE traps

Legal prawns — The ANOVA tests of CONE trap CPUE data found significant differences in the catch of legal prawns per trap by trap modification (Table 5). A Tukey test of the legal prawn CPUE by trap modification found that the Total traps had significantly lower catch per trap than either the Control or Bottom modified traps. The CPUE's from the Bottom traps were also significantly lower than the Control traps.

Sublegal prawns — The ANOVA tests of the catch of sublegal prawns per trap found significant differences by trap, soak, and soak/trap interaction (Table 5). A Tukey test of the significant interactions of sublegal CPUE's found that the Control trap for 24-h soak times had significantly higher CPUE's than all other combinations. The 48-h soaks of Control traps also produced significantly higher CPUE's than all Total and Bottom traps and finally that both soaks of Bottom traps showed significantly higher CPUE's than all Total traps.

ROUND traps

Legal prawns — The ANOVA tests of ROUND trap CPUE data found significant differences in the catch of legal prawns per trap by soak time and trap modification (Table 5). A Tukey test of the significant main effects revealed that legal-sized prawn CPUE's for the Pursed & Side and Bottom & Side modified traps were significantly lower than the catch rates of either the Total modified or Control traps. In addition, 24-h soaks had significantly lower CPUE's than did 48-h soaks.

Sublegal prawns — An ANOVA test of the sublegal CPUE's for ROUND traps found significant differences by trap modification (Table 5). A Tukey test showed that the trap effect was caused by significantly higher sublegal CPUE's in Control traps than in all other trap variations.

WIRE traps

Legal prawns — In the ANOVA test, significant differences in CPUE's of legal-sized prawns were found by soak time and trap modification (Table 5). A Tukey test comparing the soak time effects showed that legal prawns CPUE's for 48-h soaks were significantly lower than catch rates for 24-h soaks. A second Tukey test comparing the effects of trap modifications showed that Total modified traps had significantly lower CPUE's than either the Control or Bottom traps.

Sublegal prawns — The ANOVA test of CPUE's of sublegal-sized prawns found significant differences by trap modification (Table 5). For the smaller sublegal prawns, a Tukey test by trap found significantly higher CPUE's for the Control traps than for all other trap variations. In turn, the Bottom traps also had significantly higher rates than the Total traps.

WOOD traps

Legal prawns — For WOOD traps the story remained the same in that an ANOVA test found significant differences by trap modification (Table 5). A Tukey test of trap modification CPUE's found that the legal number of prawns per trap was significantly lower in the Slot, Bottom, and Panel traps than in Control or Tunnel traps. The legal prawn CPUE's of the Tunnel traps were also significantly lower than the Control traps.

TABLE 5. ANOVA test results of the square root transformed number per trap of CL ≥ 30.0 mm and CL < 3.0 mm prawns caught as a dependant variable against escape modification and soak time according to trap variation. *$P < 0.05$.

		Legal prawns			Sublegal prawns		
Trap	Source	df	Statistic	P	df	Statistic	P
CONE	Soak time (S)	1	3.10	0.0799	1	24.97	0.0000*
	Modification (M)	2	54.72	0.0000*	2	209.95	0.0000*
	S × M	2	0.13	0.8780	2	8.00	0.0005*
ROUND	Soak time (S)	1	6.74	0.0098*	1	1.89	0.1701
	Modification (M)	4	4.41	0.0017*	4	56.69	0.0000*
	S × M	4	0.89	0.4717	4	1.17	0.3218
WIRE	Soak time (S)	1	11.07	0.0011*	1	0.35	0.5536
	Modification (M)	2	13.54	0.0000*	2	275.20	0.0000*
	S × M	2	1.07	0.3463	2	0.57	0.5661
WOOD	Soak time (S)	1	0.37	0.5455	1	15.62	0.0001*
	Modification (M)	4	29.10	0.0000*	4	221.53	0.0000*
	S × M	4	2.00	0.0945	4	6.13	0.0001*

Sublegal prawns — The ANOVA test of CPUE's for sublegal prawns showed significant differences by trap modification, soak time, and soak/trap interaction (Table 5). A Tukey comparison by interaction of the sublegal prawn CPUE's found that both soak times of Control traps had significantly higher CPUE's than all other soak/trap combinations. In addition, for Control traps, the 24-h soak times provided significantly higher CPUE's than the 48-h soaks.

Discussion

Developing effective escape mechanisms for the variety of traps used in British Columbia's prawn trap fishery has proven to be a very complex task. We already know (Boutillier and Sloan 1988) that by modifying mesh size in prawn traps, it is possible to influence the size and age structure of catches. The present study has shown that selection effectiveness of escape modifications depends on not only the size of material used, but also the type of construction material used, its placement on the trap, and soak time.

Size of Modification Material

Assuming that the selection ogives for the escape-modified traps are symmetrical, Pope (1975) stated that the 50% point of the selection curve corresponds to the mean selection length. For the size of escape material used, i.e. 44-mm (stretched measured between knots) nylon web mesh, 22 × 22 mm wire mesh, and 16-mm slots, it is evident, from the 50% selection lengths (Table 4), as well as the significantly reduced CPUE's of legal prawns in many of the escape-modified traps, that the material allows for escapement of prawns well above the 30.0-mm legal size limit.

For slot modifications, the maximum prawn width in relation to slot width is considered the limiting body dimension affecting escapement. In this set of experiments, slot modifications were plagued with the same problem that Krouse and Thomas (1975) found for American lobsters, *Homarus americanus*, in that wooden slots lose their original dimensions over time. The dimensions of the slots for five of the WOOD-Slot traps were measured after the study. The wooden sides had warped to change slot size from their original 16 mm to a range of 15–20 mm in width. To overcome this problem in the lobster fishery, Krouse and Thomas (1975) suggested that the slots should be fabricated from a durable material and meet the following criteria: (1) easily installed, (2) of modest cost and (3) able to retain their original dimensions over time. These same recommendations hold true if we were to adopt the use of slots to control selectivity of solid-sided prawn traps.

Type of Construction Material

Each type of escape modification (flexible nylon and rigid wire mesh) has unique selection characteristics. From field observations (unpublished data) of prawns stuck in the mesh, prawns escape from traps tail first. For a prawn to escape through a single web or wire mesh, the girth of the animal in relation to the mesh size is probably the limiting body dimension which affects escapement. As evident in Table 4, the flexible nylon mesh selected for larger prawns (the average 50% retention size of 35.1 mm CL) than did the equivalent-sized rigid wire mesh (the average 50% retention size of 34.3 mm CL). Two possible explanations for this are that (1) the web mesh, because of its flexibility, conforms to the elliptical shape of the prawn girth allowing larger animals to escape than would the rigid wire mesh or (2) since a bale of web is known to have a certain amount of variability, e.g. 29-mm web may vary in size from 25 to 32 mm, enough of the web may be larger than the 44-mm size to account for the selection of a larger size of prawn.

Placement of Modification on the Trap

For partially modified traps, the location of escape material on the trap significantly affects selection. In the mesh-covered traps modified with escape material only on the bottom (CONE-Bottom, WIRE-Bottom), the escapement of small prawns was significantly hampered and less consistent relative to totally modified (CONE-Total or WIRE-Total) traps. This was evident in significantly higher catch rates of sublegal prawns and size selection ranges for the CONE-Bottom and WIRE-Bottom traps which ranged 49–82% larger than the equivalent totally modified traps. This restricted escapement may be because the large mesh in the CONE-Bottom and WIRE-Bottom traps is only accessible to the prawns during the relatively short period of

trap retrieval, while the fully modified traps permit continuous escapement. In the solid-sided traps, the WOOD-Bottom trap sublegal CPUE's were not significantly different from other WOOD escape-modified traps. A possible explanation is that an open-mesh bottom on an otherwise solid-sided trap causes instability when the trap is sinking. Therefore, when a trap settles, the mesh-covered side of the trap may be on the bottom, a side, or the top. If the mesh side lands on a side, or the top, then the mesh will be available for escapement while the trap is fishing and not just during retrieval as with the other bottom modified traps.

The WOOD-Tunnel and WOOD-Slot traps are similar to the CONE-Bottom and WIRE-Bottom traps in that the selection range for both the 24- and 48-h soak times is large relative to other modified trap selection ranges. This suggests that these escape modifications have not achieved the minimum stable selection range of the escape material, under the fishing conditions used in this experiment. This is understandable for both bottom modified traps, as sorting time is most closely related to retrieval time. In the case of WOOD-Tunnel traps, it may be a function of the escape material in an inefficient location, i.e. (1) the angle of the escape material in the tunnels may inhibit escapement or (2) the escape material available on the bottom perimeter of the WOOD-Tunnel traps is only about half that available on other modifications.

Soak Time

For many of the traps with a web mesh escape covering, the mean size of the prawns retained increased significantly with soak time. It appears that a longer soak time affords small prawns a greater opportunity to escape. This seems especially true for traps which are only partially modified. With the exception of the WOOD-Tunnel and WOOD-Slot traps, partially modified traps that allow escapement while fishing, i.e. ROUND-Panel, ROUND-Pursed & Side, ROUND-Bottom & Side, WOOD-Panel, and WOOD-Bottom, show a reduced selection size range with increase soak time. Totally modified traps, i.e. CONE-Total, ROUND-Total, and WIRE-Total, all have similar selection ranges for 24- and 48-h soaks, indicating that they reached a minimal consistent selectivity range sooner than traps with smaller escape panels. Even the control traps for the WOOD and CONE designs showed that longer soak time increased escapement of sublegal prawns, as was attested by the significantly different catch rates and length distributions of the 24- and 48-h soaks. Not only did the longer soak time have a beneficial effect on the escapement of sublegal prawns of many of the mesh modified traps, but it also significantly increased the catches of legal prawns in the ROUND traps, similar to the increases seen by Boutillier and Sloan (1988). The largest catches of legal prawns were in totally modified traps soaked for 48 h. This apparent increase of legal prawns may have been a function of longer soaks allowing greater ingress of larger prawns, which do not readily escape, acting in conjunction with the escape of small prawns which would alleviate trap saturation and, possibly, agonistic encounters.

For WIRE traps, increased soak time had almost the opposite effect of that seen in web-modified traps. It appears that the smaller sublegal prawns cannot escape as readily as legal prawns from the WIRE-Control traps, i.e. through the tunnel entrances. As such, we find that the catch of sublegal prawns continues to increase with longer soaks. In this instance, ingress of sublegals is greater than the low escape rate, while the catch of legals decreases because ingress is being reduced due to trap saturation, and escape rates relative to ingress rates remain high. It is unclear why escape rates from WIRE-Control traps are reduced for smaller prawns. The only obvious explanation is that the inside opening on the web-covered entrances is smooth, while the wire traps often have sharp wire projections along the inside edge which may discourage small prawns from escaping.

Conclusion

When designing escape modifications for prawn trap gear to provide selection at the 30.0-mm minimum size limit, there are a variety of factors to keep in mind. To employ traps totally covered with escape material, we must use a flexible nylon web <44 mm or a rigid wire material $<22 \times 22$ mm which will select for prawn closer to the minimum size limit. The size of material will itself depend on whether it is a flexible nylon mesh or a rigid wire mesh. To utilize traps with partial modifications, it will be important to firstly take into account that if the material is the size determined to be appropriate for the totally modified traps, escape modifications must be large enough and in an effective location such that escapement is equivalent to the totally modified traps. Secondly, if the right size of material is not available for escape modifications, then it will be necessary to use a larger material and compensate for some of the legal catch loss by partially modifying the traps in some of the inefficient locations and in amounts that hamper the escapement. Soak time plays a role in sorting and it will be important to develop escape modifications that select at similar rates for the most common soak time used by industry, i.e. 24 h (Boutillier and Sloan 1987).

The trap modification licence conditions that came into effect in 1988 for the British Columbia prawn fishery were developed on the basis of this study.

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An Electrophoretic Study of Spanish Sardine Suggests a Single Predominant Species in the Eastern Gulf of Mexico, *Sardinella aurita*

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Specimens of *Sardinella* obtained from four sites around Florida, USA, were compared electrophoretically with 41 Brazilian specimens at between 36 and 41 presumptive genetic loci in an attempt to determine whether two electrophoretically distinct species of Spanish sardine are present in the eastern Gulf of Mexico. The study found no electrophoretic evidence for two species either in Florida waters or in waters off of Brazil, with both areas predominantly, if not exclusively, represented by *S. aurita* Valenciennes. Very low polymorphism in *S. aurita* hindered extensive comparisons of allelic frequencies between Florida and Brazilian specimens; however, significant differences among allele frequencies were detected between Florida populations although not between Florida and Brazilian populations.

On a fait l'étude comparative de spécimens de *Sardinella* provenant de quatre emplacements des environs de la Floride (É.-U.) et de 41 spécimens du Brésil; il s'agissait de soumettre à l'électrophorèse de 36 à 41 loci génétiques présumés afin de déterminer s'il y a deux espèces de sardines d'Espagne électrophorétiquement distinctes dans l'est du Golfe du Mexique. L'étude n'a révélé aucun signe électrophorétique permettant de dire qu'il y a deux espèces dans les eaux floridiennes ou dans les eaux brésiliennes, les deux régions étant représentées essentiellement, sinon exclusivement, par *S. aurita* Valenciennes. En raison du très faible polymorphisme de *S. aurita*, il a été difficile de faire des comparaisons étendues de fréquences alléliques entre les spécimens de Floride et ceux du Brésil; néanmoins, il est ressorti des différences de fréquence allélique significative entre les populations de la Floride, bien que non pas entre les populations de la Floride et celles du Brésil.

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Spanish and Brazilian sardines, *Sardinella aurita* Valenciennes and *S. brasiliensis* (Steindachner), have been reported to occur sympatrically in the western Atlantic between the Gulf of Mexico and southern Brazil (Hildebrand 1963; Whitehead 1973, 1985; Johnson and Vaught 1986). However, commercial fishing for Spanish sardine in Florida waters has been presumed to exploit only a single species, *S. aurita* (Low 1973; Johnson and Vaught 1986), with essentially no acknowledged contribution to the fishery from catches of *S. brasiliensis*. Evidently, the difficult-to-use taxonomic characters which supposedly distinguish Spanish and Brazilian sardines (Whitehead 1973, 1985) have caused confusion over the extent of their supposed sympatry as well as doubt about their specific distinctiveness.

There apparently is no published documentation of *S. brasiliensis* in Florida waters which includes voucher specimens fully referenced by a recognized fish taxonomist. Whereas Hildebrand (1963) referred to specimens of *S. brasiliensis* from the Gulf of Mexico, his study material was not, in fact, connected to any United States National Museum (USNM) catalog number. His discussion was based chiefly on specimens from Port-of-Spain, Trinidad, in the southern Caribbean. Likewise, Whitehead (1973) listed no material of *S. brasiliensis* from the Gulf of Mexico which he examined directly and only cited unpublished data of C. Roithmayr (U.S. National Marine Fisheries Service, Pascagoula, MS) in discussing the Gulf range of *S. brasiliensis*. Conversely, Low (1973) determined that only *S. aurita* is represented around Florida's Biscayne Bay based on gill-raker counts of his specimens. Whereas *S. brasiliensis* as large as 162 mm standard length (SL) would be expected to possess between 160 and 180 gill rakers (Whitehead 1973), Low (1973) found no specimens this large with more than 150 gill rakers.

The possible, if yet undocumented, occurrence of two common but cryptic species of *Sardinella* in the eastern Gulf of Mexico poses a potential problem for the successful management of the Spanish sardine fishery in the Gulf of Mexico as well as in the Caribbean and southwestern Atlantic. Thus, our objective in this research was to seek evidence of a second sardine species (*S. brasiliensis*) in the eastern Gulf of Mexico sardine fishery occurring at high enough levels of representation to affect management decisions. In doing so, we have used electrophoretic techniques to search for genetic evidence of two species because the chief taxonomic character in present use, the number of gill rakers on the lower limb of the first gill arch, varies with standard length in both species and is of no use in separating specimens smaller than 120 mm SL (Whitehead 1973).

In conducting this study, we have assumed that mixed collections of cryptic but sympatric fish species (as in a two-species fishery) have a certain likelihood of being electrophoretically identifiable even by opportunistic (i.e. nonrandom) sampling by the occurrence of fixed (nonrecombinative) alternate alleles. Such has been observed in previous studies of fishes

(e.g. Shaklee and Tamaru 1981; Wilson and Waples 1983). The likelihood of detection by this method should increase with increasing numbers of specimens and presumptive genetic loci surveyed.

Materials and Methods

Specimens of *Sardinella* sp. were obtained from four main sites along the Florida coast and from one site off Santos, Brazil, between June 1988 and September 1989 (Fig. 1). Sites in the Gulf of Mexico included the Florida Panhandle region off Panama City and Port St. Joe, the Tampa Bay region, and Charlotte Harbor; the Florida Atlantic coast was sampled near West Palm Beach. The first two Gulf sites and the North Atlantic site were chosen to take advantage of commercial catches of sardines in those regions. Also, a previous, unpublished, comparative morphometric study of specimens from those areas conducted by A. Johnson (U.S. National Marine Fisheries Service, Panama City, FL) and reevaluated (R. R. Wilson and M. Tringali, unpubl. data) indicated significant morphometric differences in specimens from those sites. Charlotte Harbor was included because of opportunistic catches of *Sardinella* there by cast-netting.

To cover the possibility that the two putative species might be present in different relative abundances off Florida at different times of the year, we obtained specimens throughout the year (fall 1988 through fall 1989) as possible. However, a weak commercial season in 1989 precluded thorough sampling throughout the year as desired. We were essentially unable to obtain specimens in each summer month at any one site in the Gulf of Mexico.

Specimens obtained from the Atlantic coast of Florida were included to serve as a "control" for genetic patterns (i.e. electrophoretic mobilities of presumptive gene products) attributable uniquely to *S. aurita*. This would assist our recognition of a mixed-species sample. No *S. brasiliensis* have been reported from the Atlantic seaboard of the United States, only the Gulf (Low 1973; Whitehead 1985). Similarly, specimens from off Santos, Brazil, (24°10′S, 46°24′W) were included to serve as a "control" for genetic patterns attributable uniquely to *S. brasiliensis* which is supposedly very common off Brazilian shores, although *S. aurita* reportedly occurs there also (Whitehead 1973, 1985). Santos was chosen because an offshore purse fishery for sardine operates near there (Y. Matsuura, Instituto Oceanographi, Universidad São Paulo, pers. comm.). Specimens received from Santos arrived labeled as *S. brasiliensis*. Upon concluding the electrophoretic work, gill rakers from two Brazilian specimens were counted to confirm their nominal identity based on this character.

Most specimens were obtained frozen from commercial purse-seine boats or fish houses at the described sites. Normally, freshly pursed sardines are immediately dumped into a slurry of iced seawater and then returned to the fish house where they are immediately sorted, packed, and frozen at −40°C. All specimens from sites other than Tampa Bay and Charlotte Harbor were obtained either fresh or frozen from commercial catches in this way. The largest contingent of Tampa Bay specimens was represented by a single large catch of sardines near Longboat Key just south of Tampa Bay in February 1989. Two additional small samples were taken by cast-netting in inshore and offshore waters, one near the mouth of Tampa Bay (Ft. Desoto) in June 1989 and one some 37 km directly offshore of Tampa Bay in November 1988. Specimens were kept at −20°C while in our possession, but were normally worked up rather soon after collection.

Approximately 48 presumptive genetic loci were surveyed in extracts of brain, liver, and muscle tissue using generally applied techniques of horizontal starch-gel electrophoresis (e.g. Selander et al. 1971; Utter et al. 1987). Staining recipes followed Murphy et al. (1990). Locus nomenclature followed Shaklee et al. (1989) except that the asterisk was omitted from the locus abbreviation. If more than one zone of staining activity appeared on a gel and the presumptive loci could not be identified with certainty, zones were numbered, with the most anodal zone receiving the lowest number (i.e. 1). Alleles were designated alphabetically, with the *a* allele the most anodal, *b* next, and so on. The prefixes s and m indicate loci encoding for supernatant (i.e. cystolic) and mitochondrial isozymes, respectively. Buffer systems used were Tris–citrate (pH 8.0) and lithium hydroxide (pH 8.1) of Selander et al. (1971), Tris–citrate (pH 6.9) of Whitt (1970), and amine–citrate (pH 6.1) of Clayton and Tretiak (1972).

Frozen tissue samples were thawed and homogenized in cold 0.1 M potassium phosphate buffer (pH 7.0) and then centrifuged at approximately 10 000 × *g* for 20 min at 4°C. The extracts were applied to 12% starch gels (Sigma Starch S-4501) using strips of filter paper (wicks) which were dipped in the extract, blotted on filter paper, and then applied to the gels. Extracts were refrozen and kept at −87°C for subsequent use in a manner similar to that described by Hedgecock et al. (1988). Runs were normally between 3 and 5 h at voltage settings of between 100 and 300 V depending on the buffer system used.

Data on allele frequencies at presumptive loci were organized in the Datyp = 1 format of BIOSYS-1 (Swofford and Selander 1981) and analyzed using the BIOSYS-1 program. Analytical step functions performed were VARIAB (summary of variability), HDYWBG (Hardy–Weinberg analysis), SIMDIS (genetic distance and similarity), and CLUSTER (clustering of Nei's genetic distance estimates). The log-likelihood contingency test *G* (Zar 1974) was used to test for allelic frequency heterogeneity between populations at polymorphic loci which, after cursory review of the data, appeared likely to show significance. The log-likelihood test was first applied to Gulf of Mexico samples alone. If no heterogeneity existed, Gulf of Mexico samples were pooled and compared with those from Florida's east coast and Brazil.

Weir and Cockerham's (1984) equations were used to calculate θ (F_{st}) for several alleles at a locus to estimate the level of subpopulation differentiation at polymorphic loci showing significant heterogeneity by the *G* test:

$$(1)\quad \theta = \frac{a}{a + b + c}$$

where *a* is the observed component of variance in allele frequencies between populations, *b* between individuals within populations, and *c* between gametes within individuals. Weir and Cockerham's (1984) equations defining *a*, *b*, and *c* contain explicit corrections for uneven sample sizes. The significance of θ values were determined by χ^2 using the formulation of Workman and Niswander (1970):

$$(2)\quad \chi^2 = 2N_t\,\theta\,(k-1)$$

evaluated for $(k - 1)(s - 1)$ degrees of freedom where N_t = the total number of individuals sampled, k = the number of alleles, and s = the number of samples (i.e. subpopulations).

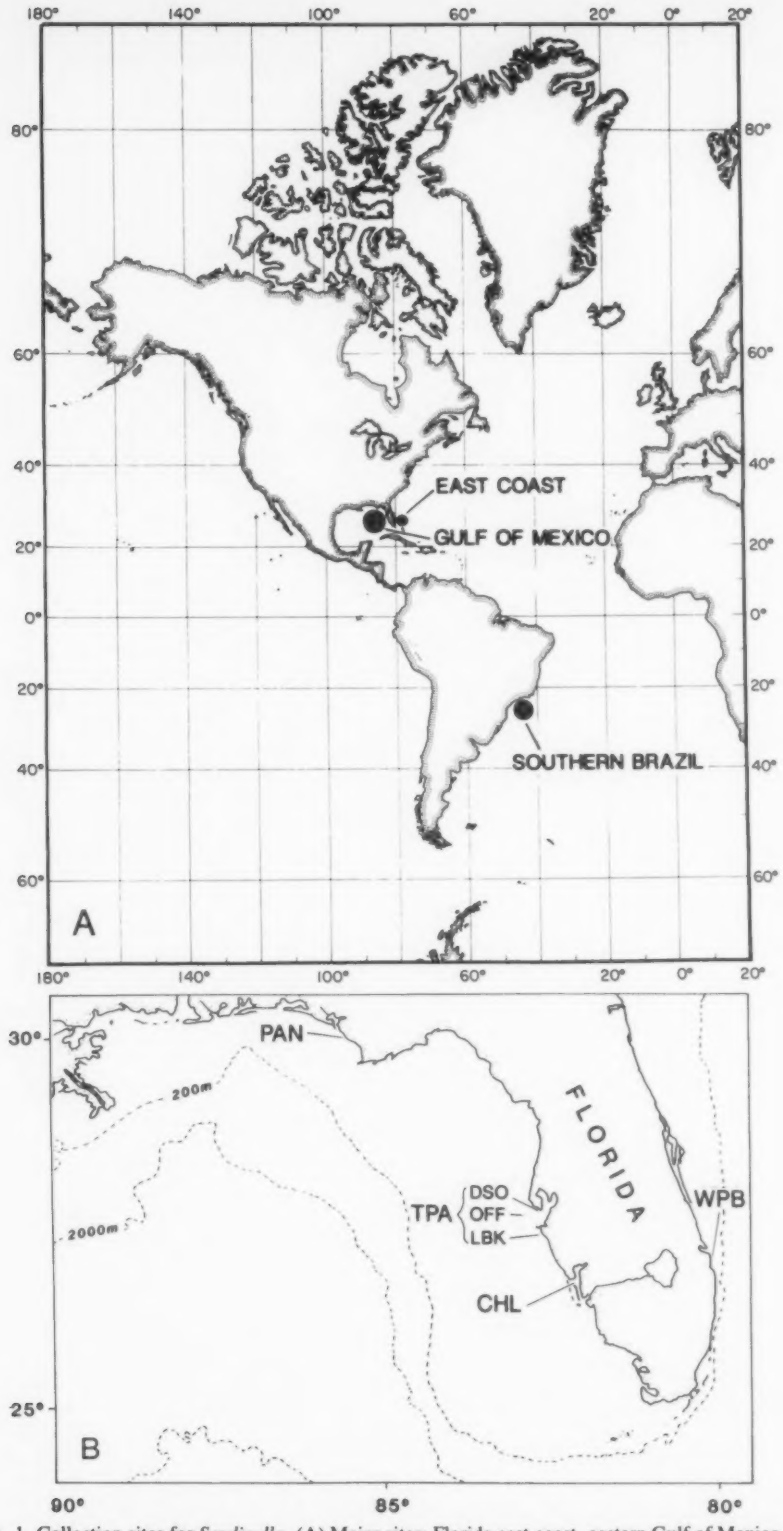

FIG. 1. Collection sites for *Sardinella*. (A) Major sites: Florida east coast, eastern Gulf of Mexico, and Santos Port, southern Brazil. (B) Sites in Florida waters: PAN = Panhandle area, TPA = Tampa Bay area, CHL = Charlotte Harbor, WPB = West Palm Beach. Tampa Bay subpopulations: DSO = Ft. Desoto, OFF = Offshore, LBK = Longboat Key.

TABLE 1. Summary of geographic and temporal coverage for collections of *Sardinella* specimens.

Month and year	Site	No. collected	No. examined
June 1988	Charlotte Harbor, FL	47	47
Sept.–Oct. 1988	Panhandle Area, FL	>200	87
Nov. 1988	Offshore, Tampa Bay, FL	21	21
Feb. 1989	Longboat Key, Tampa Bay, FL	>200	151
May 1989	West Palm Beach, FL	>200	50
June 1989	Ft. Desoto, Tampa Bay, FL	20	20
Aug. 1989	Panhandle Area, FL	40	24
Sept. 1989	Santos, Brazil	41	41
Total			441

TABLE 2. Presumptive genetic loci studied in *Sardinella*. The prefixes *m* and *s* refer to mitochondrial and supernatant isozymes. An asterisk indicates a buffer system to which allele codes refer for polymorphic loci.

Locus	Tissue	Buffer[a]
mAAT-A	Muscle	TC 8.0, TC 6.9, AC 6.1
sAAT-A	Muscle	TC 8.0*, TC 6.9
sAAT-B	Liver	TC 8.0, TC 6.9
ACPH-A	Brain, liver	TC 8.0, AC 6.1*
ADH-A	Liver	TC 8.0
ADH-B	Muscle	TC 8.0
AK-A	Muscle	TC 8.0
ALD-C	Brain	TC 8.0
CK-A	Muscle	TC 8.0
CK-B	Brain	TC 8.0
CK-2	Brain	TC 8.0, AC 6.1
GAPDH-A	Muscle	TC 8.0
GAPDH-B	Brain	TC 8.0
G3PDH-A	Muscle	TC 8.0
G3PDH-B	Liver	TC 8.0
GPI-1	Muscle	TC 8.0, TC 6.9
GPI-2	Muscle	TC 8.0*, TC 6.9
FUM-A	Muscle	TC 8.0
mICDH-A	Muscle	TC 8.0
sICDH-A	Liver	TC 8.0, TC 6.9*
IDDH-A	Liver, brain	TC 8.0
IDDH-1	Brain	TC 8.0
LDH-1	Muscle	TC 8.0
LDH-2	Muscle	TC 8.0
LDH-3	Muscle	TC 8.0
mMDH-A	Muscle	TC 8.0, TC 6.9
sMDH-B	Muscle	TC 8.0, TC 6.9*
M6PI-A	Muscle	TC 8.0
PGM-B	Brain	TC 8.0
PGDH-A	Muscle	TC 8.0*, TC 6.9
PEP-1[b]	Muscle	LiOH
PEP-2[c]	Muscle	LiOH
Proteins, 1–5	Muscle	LiOH
SOD-A	Muscle, brain	TC 8.0, TC 6.9
TPI-1,2	Brain	TC 8.0
XDH-A	Liver	TC 8.0

[a]TC 8.0 = Tris–citrate, pH 8.0 (Selander et al. 1971); TC 6.9 = Tris–citrate, pH 6.9 (Whitt 1970); AC 6.1 = amine–citrate (Clayton and Tretiak 1972); LiOH = lithium hydroxide, pH 8.1 (Selander et al. 1971).

[b]Substrate used was L-leucyl-L-tyrosine.

[c]Substrate used was L-leucylglycyl-glycine.

Results

Several hundred *Sardinella* specimens representing a wide range of standard lengths were obtained in Florida waters at various times of the year to produce the minimum desired spatial and temporal coverage (Table 1). Of these, 400 specimens from Florida and 41 specimens from off Santos, Brazil, were surveyed electrophoretically. However, the gill-raker counts (lower limb of first arch) for the two Brazilian specimens counted were 136 and 146 at standard lengths of 153 and 166 mm, respectively. These counts are in the range expected for *S. aurita* (Whitehead 1973; Low 1973).

Of the 48 presumptive loci attempted, 41 were resolved with enough staining and reading consistency to generate a reliable data base (Table 2). The mean sample size per locus was 93.5 from the Florida Panhandle, 164.3 from Tampa Bay with all three subsamples pooled, 38.4 from Charlotte Harbor, 44.7 from West Palm Beach, and 36.5 from Santos, Brazil, totalling 377.4 for the 41 presumptive loci examined here. The number of polymorphic loci observed varied among populations, but most of these loci had common alleles in excess of 95%, the rarer alleles being quite rare (Table 3). If only those loci in which the frequency of the most common allele is not greater than 95% are counted as polymorphic (i.e. the 95% criterion), then polymorphism in *Sardinella* falls between 4.9 and 7.3% of the presumptive loci surveyed, depending on population. The mean heterozygosities of Florida *Sardinella* varied between 2.0 ($\pm$1.1) and 2.7 ($\pm$1.9)%, with that of Brazilian *Sardinella* at 2.5 ($\pm$1.5)%.

The presumptive loci *EST-2* and *EST-3* of muscle appeared to be highly polymorphic on LiOH but could not be scored with accuracy so were not included in the BIOSYS-1 analysis. Two loci, *EST-1* of muscle and *G6PDH-A* of brain, showed an unusual double-banding pattern which has been previously reported in clupeids at *EST-1* (Ridgway et al. 1970). Observed variation in mobilities of enzymes encoding at *G6PDH-A* did not follow any genetic model which we were aware of, so data at that presumptive locus were omitted. There was no variation in mobilities of esterases encoding at *EST-1*, but this locus was still omitted.

Four zones of staining activity were observed from brain extracts run on TC 8.0 gels and stained for triosphosphate isomerase (TPI). Apparently, *TPI* is paralogous with two loci encoding for each of two TPI isozymes (Shaklee et al. 1989). The suggested nomenclature for these presumptive loci is *TPI-1.1* and *TPI-1.2* for loci encoding TPI-1 and *TPI-2.1* and *TPI-2.2* for loci encoding TPI-2 (Shaklee et al. 1989). Since there was no allelic variability observed at these loci and thus no real need to distinguish them, we refer to them as *TPI-1* (two most-anodal zones) and *TPI-2* (the two least-anodal zones).

The low level of polymorphism observed at most presumptive loci (except *ACPH-A* and *PEP-1*) precluded confident interpretation of tests for goodness of fit with Hardy–Weinberg expectations, since many cells had expected frequencies <1.0 (Zar 1974). χ^2 tests with pooling did little to increase the expected frequencies and, in any event, is not a preferred method. Exact probabilities given in the BIOSYS-1 output suggested deviation from Hardy–Weinberg expectations at a few loci as follows: in the Panhandle population, *IDDH-A* (p = 0.001) and *mMDH-A* (p = 0.028); in the Tampa Bay population (all subsamples combined), *PGDH-A* (p = 0.013),

TABLE 3. Allele frequencies at the 14 polymorphic presumptive gene loci for seven populations. TPA = Tampa Bay, PAN = Panhandle, CHL = Charlotte Harbor, WPB = West Palm Beach, SPB = Santos Port, Brazil. Tampa Bay subsamples: OFF = Offshore, LBK = Longboat Key, DSO = Ft. Desoto. Number of specimens scored at each locus in parentheses. ND = not determined.

	TPA						
Locus	OFF	LBK	DSO	PAN	CHL	WPB	SPB
sAAT-A							
(N)	(20)	(145)	(20)	(111)	(36)	(50)	(40)
a	—	—	0.025	—	—	—	—
b	1.000	1.000	0.975	0.991	1.000	1.000	1.000
c	—	—	—	0.009	—	—	—
ACPH-A							
(N)	(8)	(84)	(12)	(30)	(42)	(20)	(41)
a	0.250	0.345	0.292	0.317	0.286	0.400	0.305
b	0.625	0.262	0.416	0.150	0.333	0.350	0.439
c	0.125	0.393	0.292	0.533	0.381	0.250	0.256
ADH-A							
(N)	(10)	(127)	(20)	(97)	(40)	(47)	(23)
a	1.000	1.000	1.000	0.995	1.000	1.000	1.000
b	—	—	—	0.005	—	—	—
CK-B							
(N)	(19)	(138)	(20)	(103)	(47)	(49)	(41)
a	1.000	1.000	1.000	0.990	1.000	1.000	1.000
b	—	—	—	0.010	—	—	—
G3PDH-B							
(N)	(6)	(130)	(19)	(102)	(47)	(31)	(37)
a	—	0.008	0.026	—	—	—	—
b	1.000	0.961	0.974	0.985	0.979	0.952	0.986
c	—	0.031	—	0.015	0.021	0.048	0.014
GPI-2							
(N)	(20)	(148)	(20)	(81)	(8)	(38)	(41)
a	1.000	0.997	1.000	0.994	1.000	1.000	1.000
b	—	0.003	—	0.006	—	—	—
mICDH-A							
(N)	(20)	(148)	(20)	(109)	(46)	(49)	(40)
a	0.950	0.993	1.000	0.995	1.000	1.000	1.000
b	0.050	0.007	—	0.005	—	—	—
sICDH-A							
(N)		(148)	(20)	(112)	(47)	(50)	(38)
a	ND	0.003	—	—	—	—	—
b		0.997	1.000	1.000	1.000	1.000	1.000
IDDH-A							
(N)	(20)	(96)	(1)	(95)	(29)	(10)	(12)
a	—	0.036	—	0.068	0.034	—	0.083
b	1.000	0.959	1.000	0.921	0.949	1.000	0.917
c	—	0.005	—	0.011	0.017	—	—
mMDH-A							
(N)	(20)	(146)	(20)	(106)	(47)	(50)	(41)
a	—	—	0.025	0.019	0.011	—	—
b	1.000	1.000	0.975	0.981	0.989	1.000	1.000
sMDH-B							
(N)	(20)	(146)	(20)	(106)	(47)	(49)	(41)
a	1.000	1.000	1.000	1.000	0.989	1.000	1.000
b	—	—	—	—	0.011	—	—
PEP-1							
(N)	(20)	(60)	(20)	(110)	(45)	(43)	(41)
a	—	0.009	—	—	—	—	—
b	0.025	0.225	0.175	0.064	0.078	0.163	0.012
c	0.975	0.734	0.800	0.909	0.900	0.790	0.951
d	—	0.033	0.025	0.027	0.022	0.047	0.037

TABLE 3. *(Concluded)*

	TPA						
Locus	OFF	LBK	DSO	PAN	CHL	WPB	SPB
PEP-2							
(N)	(20)	(158)	(20)	(99)	(46)	(50)	(41)
a	—	0.006	—	0.010	0.022	—	—
b	0.950	0.988	1.000	0.990	0.967	1.000	0.976
c	0.050	0.006	—	—	0.011	—	0.024
PGDH-A							
(N)	(14)	(85)	(20)	(110)	(47)	(50)	(40)
a	0.071	0.006	—	—	—	—	—
b	0.929	0.994	1.000	0.977	1.000	1.000	0.962
c	—	—	—	0.023	—	—	0.038

mICDH-A ($p = 0.016$), and *PEP-1* ($p < 0.0001$); in the Charlotte Harbor population, *ACPH-A* ($p = 0.002$).

Apparent deviations at *IDDH-A*, *PEP-1*, and *ACPH-A* but not at the other presumptive loci are probably artefactual. The highly significant deviation at *IDDH-A* in the Panhandle population appears to have resulted only from one, possibly two, misscored heterozygotes, i.e. scored as homozygotes of the uncommon allele. The apparent deviation at *PEP-1* is probably due to misscoring some of the *PEP-1*b/c* heterozygotes as homozygous for *PEP-1*c/c*, although this misscoring seems to have been less a problem in the other populations. Similarly, the apparent deviation at *ACPH-A* is probably due to scoring *ACPH-A*b/c* heterozygotes as either *ACPH-A*b/b* or *ACPH-A*c/c* homozygotes. Scoring errors are not responsible for the outcome at the remaining presumptive loci, since staining was very clear and the heterozygotes easily seen. The simple χ^2 test at *ACPH-A*, applicable in this case since no cells had expected frequencies <1.0, showed $p = 0.023$ with an over abundance of homozygotes for *ACPH-A*c/c* indicated.

Upon segregating the three subsamples forming the Tampa Bay sample, allele frequencies at *PEP-1* remained far from Hardy–Weinberg expectations in the Longboat Key sample ($p = 0.003$) but not in the other two populations. Significant deviation remained at *mICDH-A* ($p = 0.026$) and *PGDH-A* ($p = 0.037$) in the offshore sample but not in the other populations. Both of these last two deviations occurred because of the presence of homozygotes for the rarer alleles with no heterozygotes observed in the respective populations. However, in considering all *Sardinella* together, heterozygotes were noted between all alleles in at least one population, whether or not in apparent Hardy–Weinberg equilibrium. Thus, no strong evidence of two genetically distinct species of *Sardinella*, based on our stated criterion, appeared among our samples.

The log-likelihood test, *G*, was applied to *sAAT-A*, *ACPH-A*, *IDDH-A*, *G3PDH-B*, *mMDH-A*, *sMDH-B*, *PEP-1*, and *PGDH-A* for the Gulf of Mexico populations: Panhandle, offshore Tampa Bay, Ft. Desoto, Longboat Key, and Charlotte Harbor. Significant *G* statistics resulted at *mMDH-A*, *PEP-1*, and *PGDH-A* (Table 4). None of the remaining loci showed significant heterogeneity in allele frequencies after pooling the Gulf of Mexico subsamples and comparing them with samples from Florida's east coast and from Brazil. Perhaps coincidently, each of the three loci above having significant *G* tests had allelic frequencies differing significantly from Hardy–Weinberg expectations in at least one population by the exact test.

TABLE 4. Summary of log-likelihood (G) contingency tests and Wright's F-statistics (θ) for *Sardinella* populations at selected presumptive loci. OFF = offshore Tampa Bay, LBK = Longboat Key, Tampa Bay, Gulf = Gulf of Mexico. NS = not significant.

Locus	Sample groupings	G or θ	p
sAAT-A	All Gulf	$G = 10.0$	NS
	All with Gulf pooled	$G = 1.44$	NS
ACPH-A	All Gulf	$G = 7.95$	NS
	All with Gulf pooled	$G = 7.69$	NS
G3PDH-B	All Gulf	$G = 8.63$	NS
	All with Gulf pooled	$G = 5.92$	NS
IDDH-A	All Gulf	$G = 8.02$	NS
	All with Gulf pooled	$G = 3.20$	NS
mMDH-A	All Gulf	$G = 13.0$	$0.01 > p > 0.005$
	All Gulf	$\theta = 0.003$	NS
sMDH-B	All Gulf	$G = 3.32$	NS
	All Gulf	$\theta = 0.014$	$0.05 > p > 0.025$
PEP-1	All Gulf	$G = 31.4$	$0.005 > p > 0.001$
	All Gulf	$\theta = 0.053$	$p < 0.001$
	Gulf minus LBK[a]	$\theta = 0.014$	NS
PGDH-A	All Gulf	$G = 19.8$	$0.05 > p > 0.025$
	All Gulf	$\theta = 0.013$	$0.05 > p > 0.025$
	Gulf minus OFF[a]	$\theta = 0.007$	NS
	All minus OFF[a]	$\theta = 0.008$	NS

[a]Apparent deviation from Hardy–Weinberg expectations.

TABLE 5. Summary of Nei's (1978) genetic distance among seven populations of *S. aurita* at 36 presumptive loci.

Population	1	2	3	4	5	6	7
1. Tampa Bay, offshore							
2. Longboat Key, FL	0.004						
3. Ft. DeSoto, FL	0.001	0.000					
4. Panhandle, FL	0.005	0.001	0.002				
5. Charlotte Harbor, FL	0.002	0.001	0.000	0.001			
6. West Palm Beach, FL	0.002	0.000	0.000	0.002	0.000		
7. Santos, Brazil	0.000	0.002	0.000	0.002	0.000	0.001	

The presumptive loci *mMDH-A*, *PEP-1*, and *PGDH-A* were further tested for subpopulation differentiation using Wright's F-statistic as formulated by Weir and Cockerham (1984). *PEP-1* and *PGDH-A* had significant θ values (Table 4) at about the same or greater level of significance seen with the log-likelihood test. Removing the Longboat Key population (deviates from Hardy–Weinberg) reduced θ at *PEP-1* to a nonsignificant value. Removing the Tampa Bay offshore population (deviates from Hardy–Weinberg) and with it its relatively high representation of the *PGDH-A*a* reduced θ to nonsignificance at *PGDH-A* within the Gulf of Mexico. Adding the Brazilian population raised θ slightly at *PGDH-A* but not significantly. This lack of subpopulation differentiation is further illustrated by values of genetic distances (Nei 1978) among the seven populations (Table 5) calculated by SIMDIS. These values ranged between $D = 0$ and $D = 0.005$. Clustering of these minute distances by CLUSTER produced essentially a vertical line.

Discussion and Conclusions

A presence of two common, sympatric species of *Sardinella* in the eastern Gulf of Mexico appears doubtful from our findings here. This conclusion is based chiefly on the failure to observe any nonrecombinative alleles (i.e. alternate fixed alleles) which might suggest segregated gene pools. Since the specimens from Florida's Atlantic coast were presumed to represent only *S. aurita* Valenciennes (e.g. Low 1973; Whitehead 1973; 1985), and since our material from other sites did not differ substantially from them, we conclude that all of our material was apparently of that species. Because a subsample of specimens comprising our "control" sample from southern Brazil also had the gill-raker counts expected for *S. aurita*, it seems likely that no *S. brasiliensis*, if present, were represented among our samples from either southern Brazil or from the Gulf of Mexico. We therefore found no genetic evidence of a second common species in the Gulf of Mexico fishery for Spanish sardine. Possible alternative interpretations of this outcome are that *S. brasiliensis* is uncommon relative to *S. aurita*, essentially no fixed allozymic differences exist between the two putative species at the loci studied, or *S. aurita* and *S. brasiliensis* are conspecific.

With respect to the first interpretation, none of the authors reporting on *S. brasiliensis* have intimated it to be uncommon relative to *S. aurita* in any of the areas it supposedly inhabits. Hildebrand (1963) reported it from off Pensacola, Florida, where some of our specimens were obtained, and it is presumed the dominant species off southern Brazil (Matsuura 1986). This supposed commoness of *S. brasiliensis* is also indicated by the fact that the holotype was discovered in a museum lot of five specimens from off Rio de Janeiro in which four of the specimens were believed to be *S. brasiliensis* (Whitehead 1973). One therefore expects that even an arbitrary sample of specimens from these same areas would contain a high fraction of *S. brasiliensis*.

Regarding the second interpretation, the possibility that two good sympatric species could not be distinguished electrophoretically seems a remote one in view of other studies. Even though not all electrophoretic comparisons of even known sympatric species have discovered fixed differences such as sought by this study (Hedgecock et al. 1988), there have been enough instances where the presence of such fixed differences has resulted in the accidental discovery of cryptic species in sympatry (e.g. Shaklee and Tamaru 1981; Wilson and Waples 1983) that it can be considered a reasonable criterion, at least when relatively high numbers of loci are investigated. It is also true that the lack of strong electrophoretic differences between recognized morphotypes has been used successfully to argue for reduction of the number of nominal species recognized in a given area (Graves and Rosenblatt 1980; Humphreys et al. 1989). The 41 presumptive genetic loci surveyed here with an average sample of 377 specimens per locus should have been extensive enough to discover a modicum of evidence for genetically distinct, widely sympatric species. The presumptive loci evaluated were probably good ones, since some of these (*sAAT-A*, *mMDH-A*, *M6PI-A*, and *PGDH-A*) have successfully resolved nearly indistinguishable morphological species of the clupeid genus *Harengula* (Alberdi 1990). Also, Hedgecock et al. (1988) found that one of three Pacific species of *Opisthonema* (Clupeidae) is identifiable by a unique allele at an *Aat* locus and the other two distinguishable by very strong frequency differences at *mMDH-A*, among other loci. Thus, the third alternative interpretation, that *S. brasiliensis* might be conspecific with *S. aurita*, merits further consideration and study.

The log-likelihood (G) statistics and Weir and Cockerham's (1984) versions of Wright's F-statistics (Nei 1977; Wright 1978) used to assess subpopulation differentiation among Florida *Sardinella* require little justification. Significant values in either statistic suggest population differentiation at some level. The significant G values at *mMDH-A*, *PEP-1*, and *PGDH-A* and θ values at *PEP-1* and *PGDH-A* suggest possible genetic structuring among Florida *S. aurita*, although these outcomes might have been influenced by apparent nonequilibrium conditions in some populations or by misscoring of a few heterozygotes at *PEP-1*. There nonetheless appear to be few allelic differences among *S. aurita* populations from the western side of the North and South Atlantic, and a very low level of genetic differentiation is indicated. However, these findings substantiate the view that *S. aurita* predominates in the eastern Gulf of Mexico and raise the question as to the presence of the second putative species, *S. brasiliensis*, in that region.

Acknowledgements

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Evaluation of Alternative Models of the Coastal Migration of Adult Fraser River Sockeye Salmon (*Oncorhynchus nerka*)

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Pascual, M. A., and T. P. Quinn. 1991. Evaluation of alternative models of the coastal migration of adult Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 48: 799–810.

A set of stochastic discrete step models of individual fish movement was developed to investigate the efficiency of compass orientation as a migratory mechanism in the coastal homeward migration of Fraser River sockeye salmon (*Oncorhynchus nerka*). Ultrasonic tracking data provided empirical values for the required parameters. Alternative movement models were validated by comparing the results of Monte Carlo simulations and known features of sockeye migration: general aspect of individual trajectories, timing, success in reaching the goal, and spatial occurrence. The effect of different headings and directional precisions on the probability of success in reaching the goal were considered. The more complex models captured the essence of observed movement patterns, but the number of fish getting to the goal was lower than expected. Many "modeled" fish were lost in the complex web of channels and inlets characteristic of this area. We conclude that the preference of a compass direction is not a sufficient mechanism to explain the observed migratory behavior of Fraser River sockeye salmon in coastal areas. Other mechanisms, such as negative kinetic responses to water from nonnatal rivers or short-term learning, may prevent the fish from being trapped in complex areas.

On a mis au point un ensemble de modèles stochastiques à étapes discrètes représentant les déplacements de poissons individuels afin d'examiner l'efficacité de l'orientation au compas comme mécanisme migratoire dans la migration vers la côte du saumon rouge (*Oncorhynchus nerka*) du Fraser. Comme valeurs empiriques à attribuer aux paramètres nécessaires, on s'est servi de données de repérage aux ultrasons. On a validé d'autres possibilités de déplacements en comparant les simulations de Monte Carlo à des caractères connus de la migration du saumon rouge : aspect général des trajectoires individuelles, synchronisme, atteinte de l'objectif et occurrence spatiale. On a pris en considération l'effet de différentes destinations et précisions d'orientation sur les chances d'atteindre l'objectif. Les modèles plus complexes reproduisaient l'essentiel des déplacements observés, mais le nombre de poissons atteignant l'objectif était plus bas que prévu. Bon nombre de poissons "modélisés" se sont perdus dans le réseau complexe de canaux et de baies qui caractérise la région étudiée. Nous avons conclu que l'orientation au compas comme moyen de prédilection n'est pas suffisante pour expliquer le comportement migratoire observé chez le saumon rouge du Fraser en zone côtière. Il se peut que d'autres mécanismes, comme les réponses cinétiques négatives aux milieux autres que les eaux d'origine ou l'apprentissage à court terme, évitent au poisson de rester captif dans les secteurs complexes.

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Various mechanisms have been proposed to explain how fishes are guided during the different stages of their migrations. Some mechanisms rely on remote information such as celestial (Groot 1965; Brannon 1972) and geomagnetic (Quinn 1980) clues. Other mechanisms rely on proximal information such as kinetic responses to optimize the fishes' external environment (Leggett 1977), responses to memorized olfactory stimuli from the home river (Hasler and Scholz 1983), and selective use of tides (Arnold and Cook 1984; Dodson and Dohse 1984).

In the case of Pacific salmon, reliance on proximal information in open waters is unlikely, as the oceanographic conditions in open seas provide the fish with no regular pattern to follow (Groot and Quinn 1987). The directness of the migration led some authors to propose that salmon rely on compass (Royce et al. 1968) or bicoordinate nagivation (Neave 1964; Quinn 1984) to guide their migration. In contrast with mechanisms of migration in open waters, evidence indicates that olfaction plays a dominant role in guiding salmon during upriver migration (Hasler and Scholz 1983).

Coastal areas present the fish with a blend of oceanic and riverine conditions, within a structurally complex environment. Concurrently, the fish undergo physiological, morphological, and behavioral transformation. Thus, it was postulated that the guidance in coastal areas might be based on a combination of oceanic and riverine mechanisms (Quinn and Leggett 1987; Quinn and terHart 1987).

Individual sockeye salmon (*Oncorhynchus nerka*) of Fraser River origin returning to the spawning grounds follow one of two routes around Vancouver Island: the northern route in Queen Charlotte Strait, Johnstone Strait, and the Strait of Georgia and the southern route along the southwest coast of Vancouver Island and Juan de Fuca Strait (Fig. 1). It has been proposed that the salmon maintain a compass heading as they approach the coast and that interannual variations in timing (Blackbourn 1987) and route (Groot and Quinn 1987) are attributable to temperature-related differences in their distribution prior to migration.

In contrast with the homeward migration of adults, most smolts heading to the ocean from the Fraser River use the north-

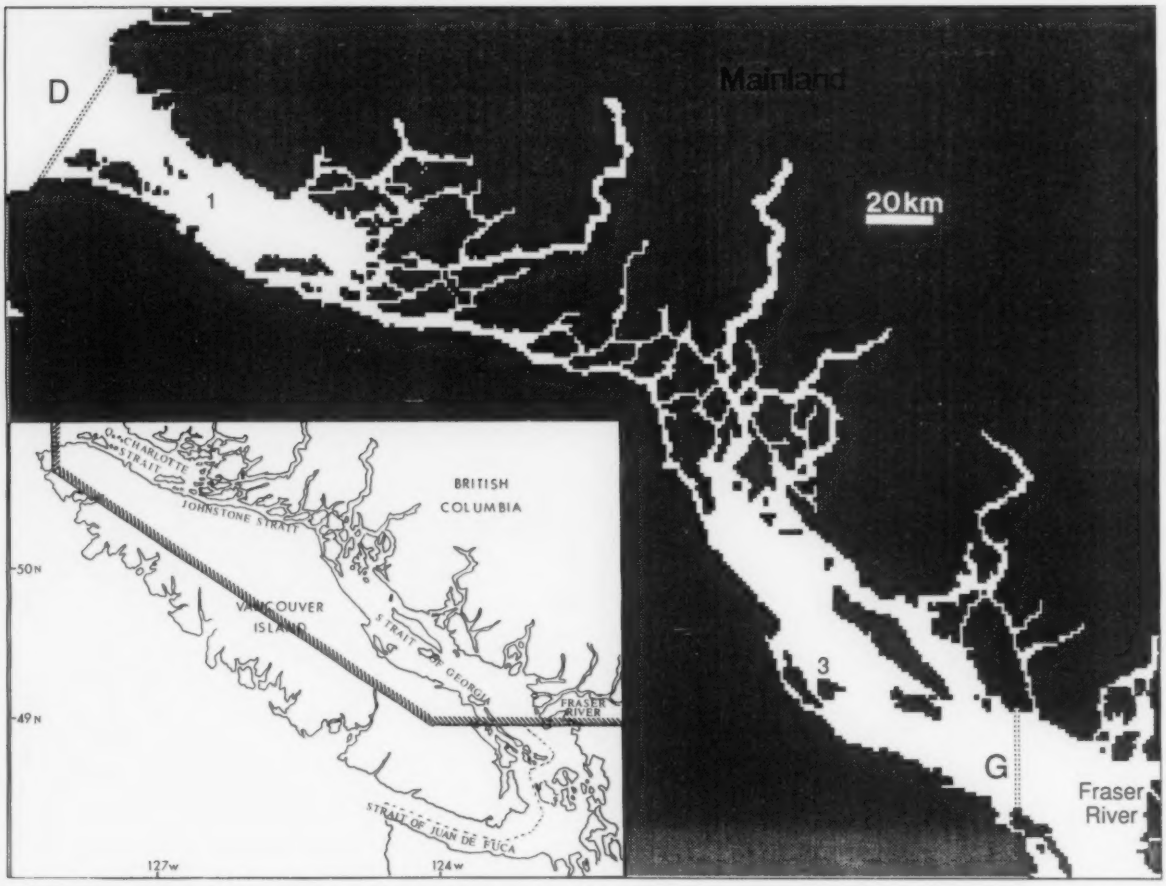

FIG. 1. Northern route to the Fraser River and the graphical representation of the binary space matrix used in the simulations (shaded = land, white = water, D = departure line, G = goal, 1 = Queen Charlotte Strait, 2 = Johnstone Strait, 3 = Strait of Georgia).

ern route (Groot and Cooke 1987). It follows that in many years, most adult sockeye reach the Fraser River travelling through unfamiliar regions, which suggests that the mechanisms guiding them in coastal areas are not based on the response to familiar spatial stimuli, i.e. "piloting" in the terminology of Griffin (1955).

Ultrasonic tracking studies performed on northern Vancouver Island during 1985 and 1986 revealed that adult Fraser River sockeye salmon had a southeast preference (the general direction of the home river: Quinn et al. 1989). The pattern of movement decisions displayed by the fish was independent of the tidal currents characteristic of this area. Moreover, the fish did not trace the shorelines, but when encountering an obstacle they often swam in the opposite direction for some time. This was proposed as a mechanism to reduce the probability of the fish being trapped in geographical enclosures such as bays and inlets.

The ultrasonic tracking data provided a powerful tool for excluding the selective use of tides or the tracing of the coastline as mechanisms of sockeye salmon migration on northern Vancouver Island. However, there are several hypotheses which are equally compatible with the observed movement behavior. The preferred direction displayed by sockeye salmon may result from a global preference of a compass direction or may be the outcome of the orientation to proximal information, such as water characteristics (e.g. temperature and salinity).

The objective of this work is to investigate whether the preference of a compass direction is an effective guidance mechanism for salmon in geographically complex coastal areas. We developed and evaluated a set of models, or "strategies", of sockeye salmon movement, which are consistent with the preference of a compass heading as a form of orientation in which no direct sensory contact with the goal itself or with known landmarks in its vicinity is used (Wallraff 1960). Stochastic models of individual movement served as the building blocks for a Monte Carlo simulation of sockeye salmon migration along the northern route to the Fraser River for each strategy. Ultrasonic tracking data of adult Fraser River sockeye salmon in northern Vancouver Island provided empirical values for the required simulation parameters (see Quinn and terHart 1987; Quinn 1988; Quinn et al. 1989 for a detailed description of this data set).

Alternative strategies were compared with known features of sockeye migration: general aspect of individual trajectories, timing, success in reaching the goal, and spatial occurrence. Within each movement strategy, effects of different headings and directional precision on the probability of success in reaching the goal were assessed.

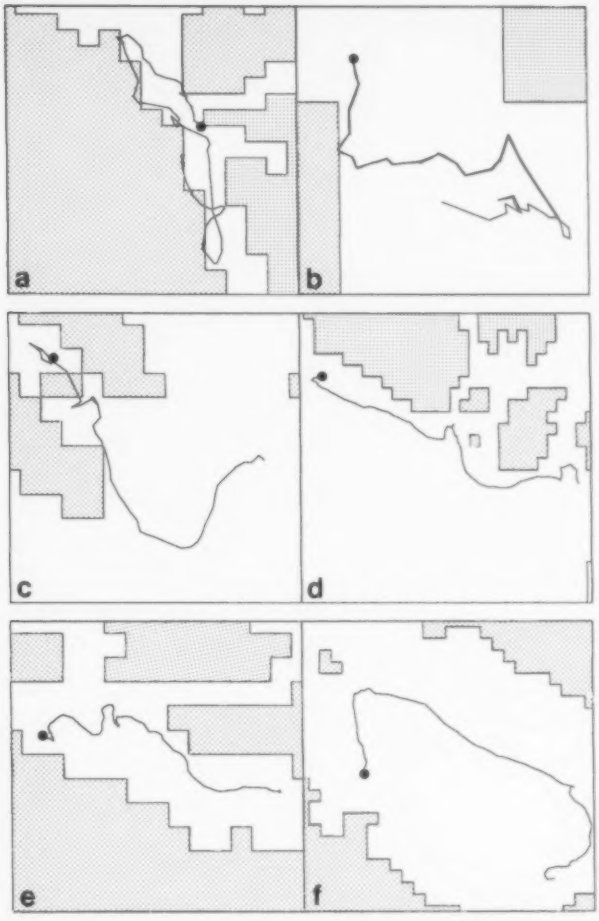

FIG. 2. Trajectories of six sockeye salmon as revealed by ultrasonic tracking (from Quinn and terHart 1987; Quinn et al. 1989). ● = release point.

Methods

Model Structure

The simulation models are based on two components: a grid representing the area under consideration and a set of rules for fish movement over this space (departure point, speed, response to the coast, direction, and endurance). The area under consideration extends from 123 to 129°W and from 49 to 51°20′N. This space was schematized as a binary matrix of admissible (water) and inadmissible (land) places for the fish. The "grain" of the grid was chosen to be as fine as possible within the limits of computer feasibility: 220 × 360 squares of 1.176 km on each side (Fig. 1).

Fish movements were simulated by a probabilistic discrete step model, characterized by statistical distributions of the direction and step length between successive movements (Siniff and Jessen 1969). Step length substitutes for speed in discrete terms; given a specific time interval, the step length is the effective distance travelled by the fish during this time. The movement of a simulated fish in a time interval results from the trigonometric combinations of values for direction and step length randomly chosen from these distributions. For example, if at time t the fish is located at the point with coordinates (X_t, Y_t), and the step length between time t and time $t + 1$ is S_t, and the direction is ϕ_t degrees with respect to the north, then the position of the fish at time $t + 1$ (X_{t+1}, Y_{t+1}) is

$$(1) \quad X_{t+1} = X_t + S_t \sin(\phi_t)$$

and

$$(2) \quad Y_{t+1} = Y_t + S_t \cos(\phi_t).$$

In the models the X and Y coordinates were continuous. The discrete space matrix described above served only to delineate the boundaries between land and water, but for the purpose of the fish movement itself this space was continuous.

Ultrasonic tracking data provided a time series of the fish's positions which yielded estimates of direction and speed. These estimates are dependent on the time interval selected, i.e. the smaller the interval, the greater the similarity between the recorded and the actual trajectory (Hawkins and Urquhart 1983). The time elapsed between successive position records in the ultrasonic tracking study was typically 5 min, but time intervals of 10 min were used for the simulations in order to decrease run time.

Step length

The observed distribution of fish step lengths (swimming speeds) was unimodal (mean = 2.4 km/h), rising quickly from zero with a long right-hand tail (Quinn 1988). The gamma distribution proved to be effective for modelling this type of data (Siniff and Jessen 1969). Its density function is

$$(3) \quad f(z) = \frac{1}{\beta^{\alpha+1}\,\Gamma(\alpha+1)}\, z^{\alpha}\, e^{-z/\beta}.$$

The two parameters characterizing this function were estimated numerically, by minimizing a chi-square criteria between the observed and the expected number of counts for different intervals of step length ($\alpha = 1.45$ and $\beta = 0.126$, step length units = (grid units/10 min)). Generated values from this distribution were used as the step length (S_t in equations (1) and (2)) at each time interval.

Response to the coast

Ultrasonic tracking provides an approximate position of the fish at a scale that does not allow one to evaluate the fishes response to the coast with high precision. The fish may in fact react to the bottom slope, rocks, reefs, or coastal eddies and not to the simplified coast represented in a map. The behavior of sockeye, as perceived from the trajectories of tracked fish, was variable. However, it was evident that they did not trace the shorelines, but when encountering an obstacle they often swam in the opposite direction. The average behavior appears as a rebounding type of response, which we tried to reproduce in our model. When a simulated fish hit the coast, it rebounded with an angle equal to the incidence angle. The angle of the coast was interpolated for the general countour around the specific square in the space matrix that the fish hit. This correction attempted to minimize aberrant patterns of behavior that could arise from a fish's interaction with the "square" coast within a grid point.

Direction

The criteria for incorporating direction to the fish trajectory at each time interval is the key feature characterizing the alternative strategies. In the simplest case the direction followed by

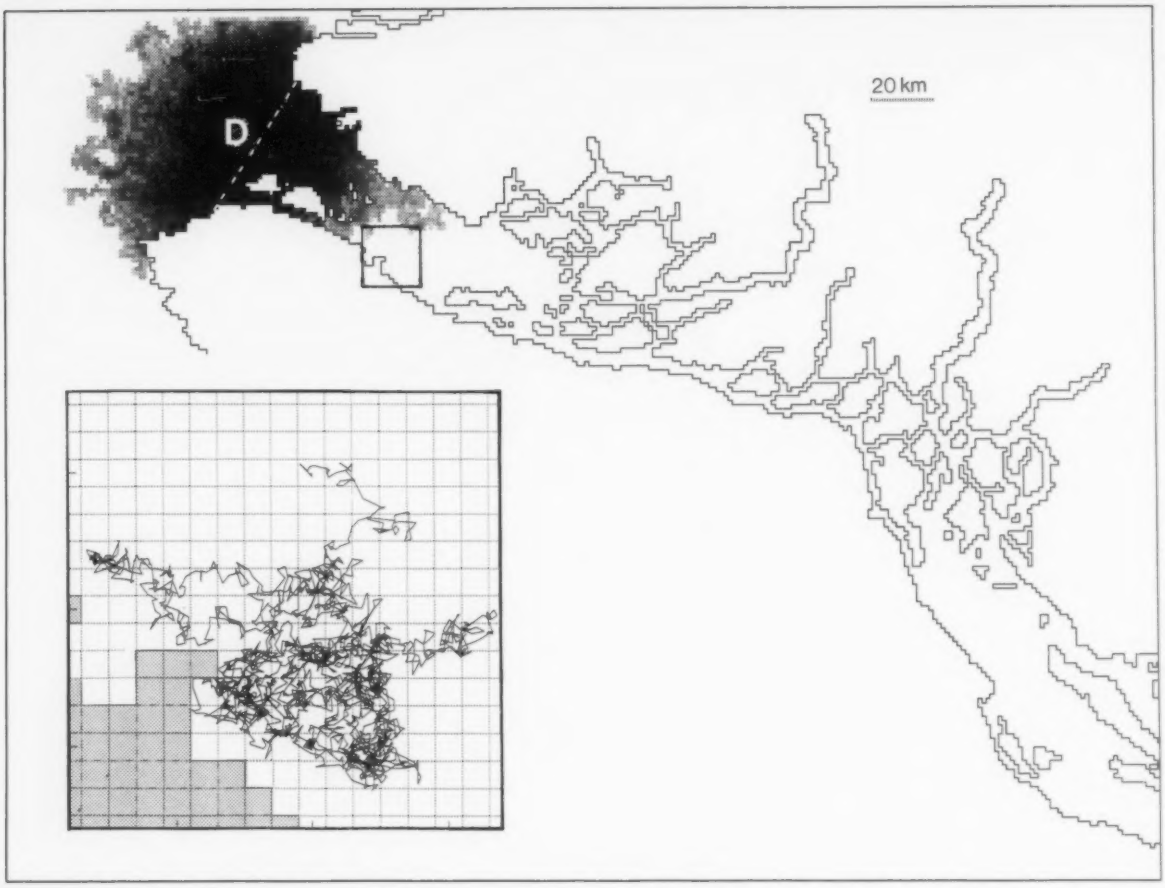

FIG. 3. Spatial distribution generated by 500 fish simulated under the *uniform* movement strategy. Intensities in the shaded area are proportional to abundances in different cells in logarithmic scale (D = departure line). The inset contains an example of an individual trajectory.

the fish at each time interval was represented by a random deviate from an uniform distribution (ϕ_t in equations (1) and (2)), taking compass values between 0 and 360°. This strategy (*uniform*) represents the lack of orientation and was included to determine the likelihood of fish getting to the goal by random search.

In the next strategy (*normal*), direction was added to the fish trajectory by modelling its heading at each time interval (ϕ_t in equations (1) and (2)) as a random deviate from a normal distribution. The mode of the distribution represents the more frequent direction in degrees with respect to the north, and in the simulations, 11 different values from 110 to 160° at intervals of 5° were tried. The directional precision varied according to four different values of the coefficient of variation (CV: 0.1, 0.2, 0.3, and 0.4). All 44 possible combinations of mean heading and directional precision were evaluated.

As an attempt to represent the fish movement more realistically, the next strategy (*inertial*) modelled the change in direction of the fish at each time interval. This movement strategy takes into account the tendency to maintain direction (Bovet and Benhamou 1988). The actual direction of the fish with respect to the north was a weighted average of a preferred heading and the past trajectory plus the change in direction. For example, if the angle of the past trajectory with respect to the north is δ, the change in direction is σ, the preferred direction is μ, with weight ω between 0 and 1, then the new direction (ϕ_t in equations (1) and (2)) is the angle of the vector with orthogonal components

$$(4) \quad x = (1-\omega)\sin(\delta + \sigma) + \omega \sin(\mu)$$

and

$$(5) \quad y = (1-\omega)\cos(\delta + \sigma) + \omega \cos(\mu).$$

Angles with respect to the north from 110 to 160° at intervals of 5° were used as the preferred heading. Four weights from 0.1 to 0.4 given to the preferred direction were used to express different degrees of directional precision. A weight of zero, meaning lack of orientation, can be used to model a second null hypothesis. The distribution of changes in direction by telemetered fish in open water was fitted by the use of a robust smoothing algorithm (Becker and Chambers 1984); 5000 deviates generated from this distribution were used in the simulations as values for σ. An empirical distribution was used because various density functions explored failed to fit properly to the peak and tails of the observed data distribution.

The last strategy considered (*escapist*), is essentially similar to the previous one, but differs in that, after hitting the coast, the fish swims for some time without orientation ($\omega = 0$). As will be exemplified later, ultrasonic tracking analysis suggests that such conduct is part of the sockeye movement behavior.

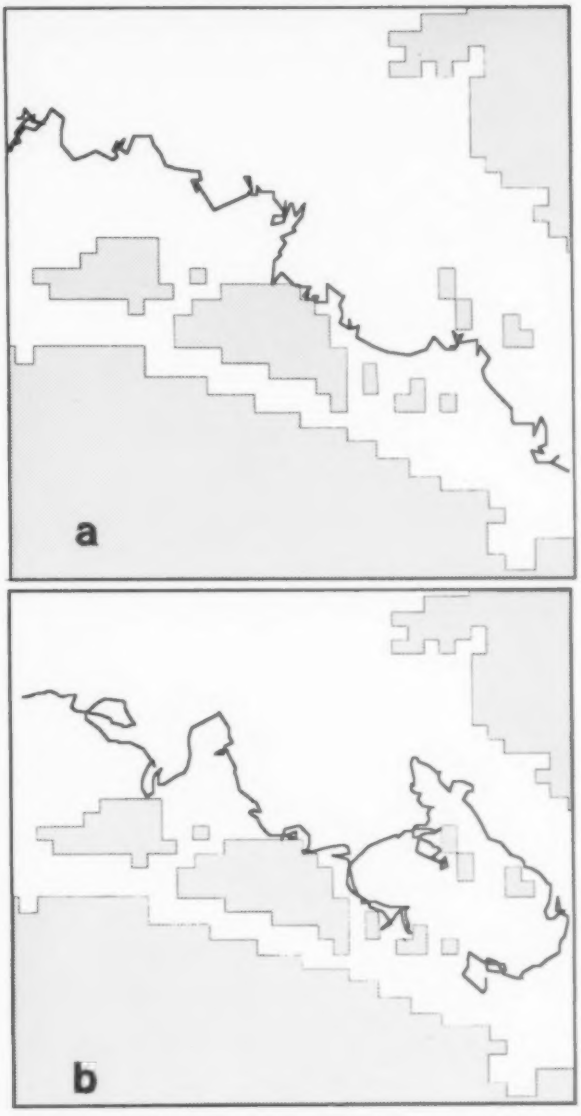

FIG. 4. Simulated trajectories generated by the (a) *normal* movement strategy for preferred direction (μ) = 125° and CV = 0.35 and (b) *inertial* movement strategy for preferred direction (μ) = 125° and weight (ω) = 0.02.

The fish were given 30 min (three time intervals in the simulations) before orientation was restored, based on inspection of the actual tracks.

Under the last two strategies the fish display a constant *average choice* of direction. However, the *realized trajectory* is not necessarily constant but a complex result of the stochasticity around the average choice and the interaction with the coast.

Departure point

The departure point for each simulated fish was randomly located on a line at the mouth of Queen Charlotte Strait (51° lat., 128° long.) (Fig. 1) at a distance of about 400 km from the Fraser River.

Goal

A vertical boundary at 45 km due west of the mouth of the Fraser River was considered to be the goal (Fig. 1). Any fish crossing this line was considered to have successfully performed the migration.

Endurance

This is the time that the fish was allowed to swim until it was considered lost. Tagging studies suggest that few sockeye salmon arrive after 30 d of migration through the northern route (Verhoeven and Davidoff 1962). A time period of 4 wk, or 4000 time intervals in the simulation, was used as the endurance time.

Program Structure, Outcomes, and Results Validation

Individual fish were allowed to run under the rules of a specific movement strategy until the endurance time elapsed, or alternatively, until they reached the goal or ran out of the boundaries of the space grid, in which case they were considered lost. This procedure was repeated 500 times for each run of the program (i.e. each parameter value combination within each strategy). The outcomes of the simulations consisted of the generated individual trajectories, the proportion of fish arriving to the goal and their timing, and the spatial distribution of the fish.

For each run of the program the number of fish reaching the goal and the migration time of each successful fish were recorded. The number of times that each cell of the space matrix was visited by a fish was also enumerated. These data generated a characteristic spatial distribution for that particular run of the program. These distributions represent the relative probability of individual cells containing a fish during the endurance time, combining the number of different fish visiting that cell and the residence time of the fish in that cell.

To evaluate the performance of the different movement strategies and different parameter values within strategies, the results of the simulations were validated by both qualitative and quantitative contrast with available information about sockeye migration. The proportion of the fish getting to the goal was compared with the estimated homing success as suggested by genetic studies (Quinn et al. 1987) and catch records (International North Pacific Fisheries Commission (INPFC) 1984). The estimated travelling time from tagging studies (Verhoeven and Davidoff 1962) was used as the standard to which the timing of the simulated fish was contrasted. Inspection of the generated trajectories under the different strategies served as a qualitative test of their merits in reproducing the tracked sockeye behavior. The examination of the verisimilitude of alternative values of preferred heading was done by a qualitative comparison of the spatial distributions generated by the simulations and the spatial distribution of catches in experimental fishing cruises (Cooke et al. 1987).

To evaluate the effect of the geographical complexity on the simulated fish movement, headings were recorded for two different sections of the northern route: the geographically complex area comprised by Queen Charlotte Strait, Johnstone Strait, and Discovery Passage and the relatively simpler Strait of Georgia (Fig. 1).

Simplifying Assumptions

We made some simplifying assumptions about fish behavior in this model. First, we modelled fish's movement in two

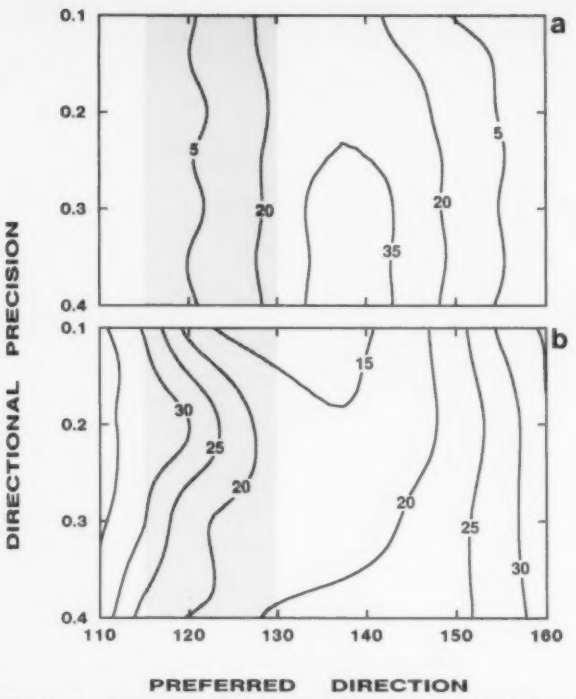

FIG. 5. Contour graphs of (a) percent of success in reaching the goal and (b) median timing in days for 500 simulated fish under the *normal* movement strategy for different values of preferred heading (μ) and directional precision (= CV of normal heading distribution). See text for interpretation of shaded areas.

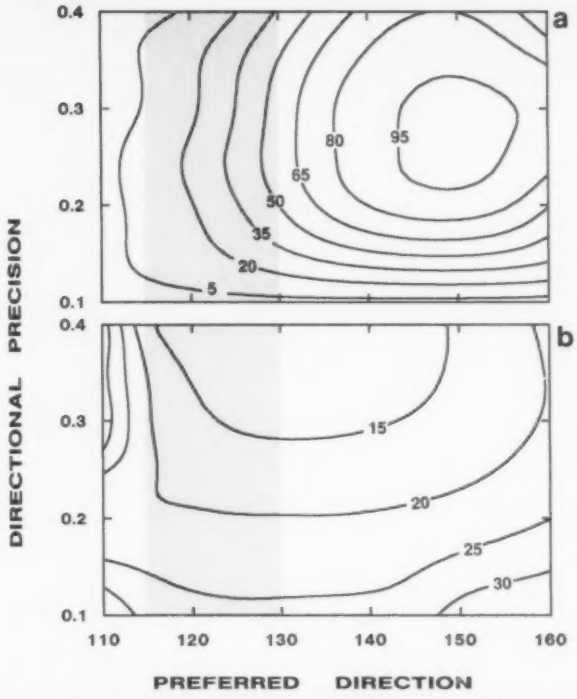

FIG. 6. Contour graphs of (a) percent of success in reaching the goal and (b) median timing in days for 500 simulated fish under the *inertial* movement strategy for different values of preferred heading (μ) and directional precision (ω = weight to the preferred direction). See text for interpretation of shaded areas.

dimensions, without regard to variation in depth of travel. Information on depth of travel is available (Quinn et al. 1989) but has not been integrated with horizontal movement.

Second, considering the reversing nature of tidal currents, we assumed that the current effects on the net movement of the fish average to zero over time. Ultrasonic tracking showed only a weak association between current direction and fish direction with respect to the water (Quinn et al. 1989). The choice of direction by the fish seems to be practically independent of the occurrence of water mass movements. However, it must be understood that this simplifies complex oceanographic processes (Thomson 1981). The currents on northern Vancouver Island are not neatly bidirectional, but are characterized by eddies and backcurrents at the spatial scale relevant for a migratory fish. This makes them both unlikely as a significant aid in the migration along these waters and impossible to model given the available information about currents in this area. Moreover, because the residual currents are opposed to the "home" direction, more than weak countercurrent orientation would be required to effect rapid travel through these regions.

The discrete step model we used assumes independence between the direction and the speed of the fish. This assumption is in conflict with observed higher speeds for directions within the quadrant heading to the home river (Quinn et al. 1989). However, the observed association was weak and we therefore decided to make the assumption of independence. This simplification is taken into account when analyzing the results. Sockeye salmon also seem to be less active at night (Madison et al. 1972; Quinn et al. 1989), another trait which is not included in the model. The distribution of step lengths used in the simulations resulted from pooling the observations for all the tracked fish, disregarding the time of the day at which the tracking took place. Since more records were available for day than for night, a slight overestimation of the fish speed in the simulations is expected.

Finally, the models assume that individual fish movements are independent of the movements of other fish in the vicinity. The behavior of the individual can, in theory, be enhanced by the behavior of the group (Larkin and Walton 1969). Sockeye salmon are at most facultative schoolers at this period of their lives. Moreover, there is an intrinsic confounding in the available information, for different individuals may converge to the same locations as a result of similar, but independent, migratory behavior. As described below, our simulations produced this type of pattern.

Results

Qualitative Assessment of the Movement Strategies

Analysis of the movement strategies must include an evaluation of their power in capturing the main features of sockeye salmon movement. One way to do this is to compare the simulated trajectories for the alternative movement strategies with those observed for tracked fish. Figure 2 shows the trajectories of six tracked sockeye. These tracks are among the longest available and typify the 30 available trajectories. Despite considerable individual variation in fish movement patterns, some general features were observed. The trajectories in open water were generally smooth; sharp turns were only

observed in cases where the fish interacted with the coast. Those fish encountering the coast neither followed the shoreline nor stayed at any point for a long time (Quinn et al. 1989). In general, they changed direction, swimming away from the coast (Fig. 2a and 2b).

The trajectories simulated under the *uniform* strategy are very unlike the observed trajectories (Fig. 3). The random headings from a uniform probability distribution generated trajectories characterized by sharp turns and very limited net movement in any direction. None of the 500 fish in the simulation advanced more than 60 km in the direction of the Fraser River (Fig. 3).

Directed strategies, on the other hand, generated more realistic trajectories (Fig. 4). The sharp turns which characterized the *normal* strategy (Fig. 4a) resulted from modelling the direction at each time interval as independent of the direction in previous intervals. *Inertial* and *escapist* strategies produced smoother trajectories than those generated by the *uniform* and *normal* strategies (Fig. 4b). Trajectories generated by *inertial* and *escapist* strategies also displayed wider turns after encountering the coast than the *normal* strategy. While the movement patterns generated by these two strategies are not remarkably different from each other, the *escapist* strategy increased the ability of simulated fish to escape from structurally complex areas. This task was poorly performed by simulated fish under the *normal* strategy.

Monte Carlo Simulation Results

The effects of the different movement strategies on the overall migration process were evaluated by Monte Carlo simulations. Instead of analyzing the behavior of an individual fish, the simulations assessed how different headings and degrees of orientation affected the probability of reaching the goal and the average time required to perform the migration, in the context of the different movement hypotheses.

Within the *normal* strategy, no combination of direction and directional precision brought over 40% of the salmon to the vicinity of the Fraser River within 28 d (Fig. 5a). For preferred headings between 135 and 145°, over 35% of the fish arrived at the goal, but this proportion declined abruptly for angles below and above these values. The median timing for those fish reaching the goal was strongly affected by the directional precision (Fig. 5b); for any preferred heading, more directed movement resulted in shorter migration times. Shortest timings were observed for headings between 120 and 145° and higher directional precision (CV < 0.2).

In contrast with the results for the *normal* strategy, under the *inertial* strategy, higher proportions of fish attained the goal (Fig. 6a). Over 95% success was observed for a preferred heading of 150° and intermediate directional precision ($\omega \sim 0.3$). This success rate declined at higher and lower headings, indicating that there is an angle that minimizes the chance of fish being caught in structurally complex regions. The proportion of fish attaining the goal also declined with higher and lower directional precision. High directionality decreased the flexibility of movement and, therefore, reduced the chance of a fish escaping from geographical "traps". On the other hand, low directional precision produced more erratic movement and little progress towards the goal.

There was a wide range of angles yielding short timing (median < 15 d) for higher directional precision (Fig. 6b). Particular combinations of heading and directional precision (e.g. 145° and $\omega = 0.35$) produced 95% success with median timing under 15 d.

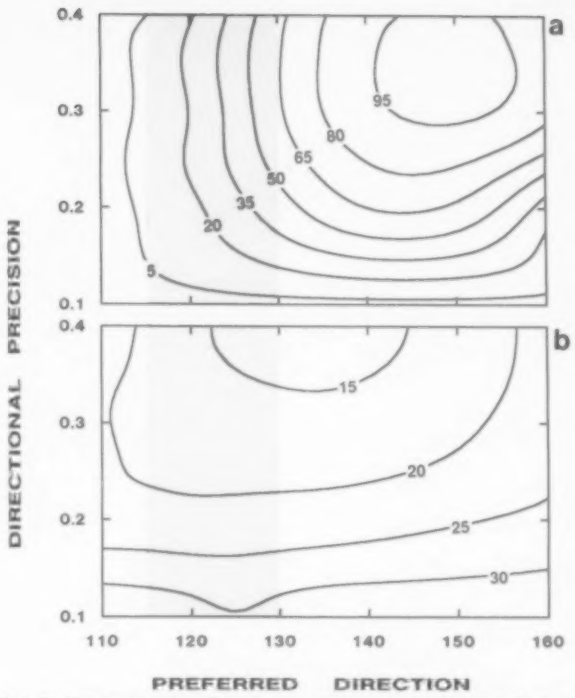

FIG. 7. Contour graphs of (a) percent of success in reaching the goal and (b) median timing in days for 500 simulated fish under the *escapist* movement strategy for different values of preferred heading (μ) and directional precision (ω = weight to the preferred direction). See text for interpretation of shaded areas.

The results for the *escapist* strategy were similar to those for the *inertial* strategy (Fig. 7), with the difference that more fish attained the goal at high levels of directional precision. This resulted from the escapement mechanism added to this strategy; highly directed movement was possible in open waters without compromising the flexibility of the fish movement in more complex areas, which was ensured by the brief period of non-directed movement after hitting the coast.

Validation of the Simulations

Spatial distribution

The spatial distributions generated by the simulations were sensitive to the preferred heading selected. Figure 8 illustrates the spatial distributions corresponding to values of preferred direction of 150 and 120° under the *escapist* strategy and for high directional precision ($\omega = 0.4$). For more southerly headings the fish occupied only the southern coasts along the route to the Fraser River (Fig. 8a). As the preferred direction was shifted eastward the fish tended to use broader regions of Queen Charlotte Strait, the inlets at the northern coast of Johnstone Strait, and the central and northern parts of the Strait of Georgia (Fig. 8b). Preferred headings of 120–110° caused most of the fish to swim into the inlets of the northern coast, and consequently, few fish reached the Strait of Georgia. Simulations for the *inertial* strategy generated similar patterns of spatial distributions for the different values of preferred heading.

The best available information about the spatial distribution of sockeye salmon in this area comes from experimental fishing

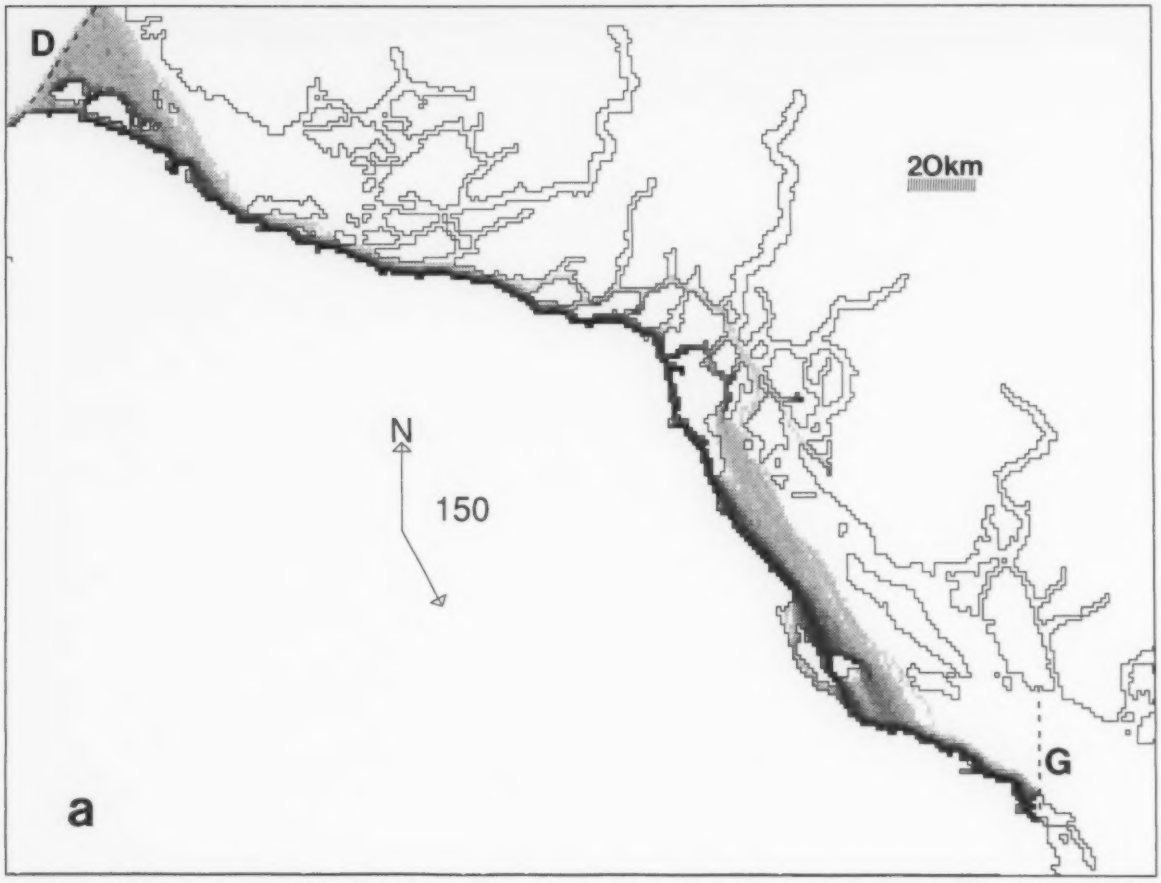

FIG. 8. Spatial distributions generated by 500 simulated fish for the *escapist* movement strategy for preferred headings (μ) of (a) 150° and (b) 120° (D = departure line, G = goal). Intensities in the shaded areas indicate relative abundances (logarithm of the number of times a cell was visited by a fish). (*Fig. 8 concluded next page*)

cruises performed in 1985 and 1986 (Cooke et al. 1987) and surveys of the distribution of fishing effort (Ledbetter 1984). The observed distribution of catches was used to evaluate the likelihood of the different preferred headings used in the simulations; those headings generating distributions compatible with the spatial pattern of fishing were regarded as more likely. Catches in the survey were high for various regions of Queen Charlotte Strait, with the highest catches obtained at the northwest coast of islands. This is consistent with Ledbetter's (1984) observation that fishing boats operating in this area concentrated along the northwest coast of islands. This distributional pattern was also generated by the simulations for the range of preferred headings 115–130° (Fig. 9). The highest catches in Johnstone Strait were obtained along the southern coast, similar to the simulation results. In the Strait of Georgia, the highest catches were obtained around the islands located in the central part of the strait, which is consistent with the concentrations of fish in these areas generated by the simulations. The mean heading displayed by ultrasonically tracked sockeye was 124° (Quinn et al. 1989). Overall, only preferred headings between 115 and 130° can be regarded as realistic. Higher and lower headings failed to generate spatial distributions consistent with the spatial pattern of catches in this region and are not supported by the observed behavior.

So far, the determination of "realistic" headings has only considered the Fraser River sockeye migration along the northern route. However, in most years, most individuals have used a different route around the southern coast of the island and through the Juan de Fuca Strait (Groot and Quinn 1987). Unfortunately, there is less detailed information available for the southern route than for the northern route. However, it can be speculated that the angle of the southern coast of Vancouver Island is an "adequate" average heading for the fish to follow. Higher (more southerly) angles would increase the probability of fish missing the Juan de Fuca Strait route; lower (easterly) angles would increase the chance of fish swimming into the inlets characteristic of this coast. The average angle of the coast with respect to the north is about 125°, within the range of preferred headings that were previously indicated as more likely for migration in the northern route.

Migration success

Presently there are no reliable estimates of the proportion of fish entering the northern route that subsequently reach the Fraser River. Results obtained from tagging experiments are highly dependent on the distribution and amount of fishing effort allocated during the process of tag recovery. Since this region is structurally very complex, there are countless potential places for the fish to go. Tag recovery rates provide only

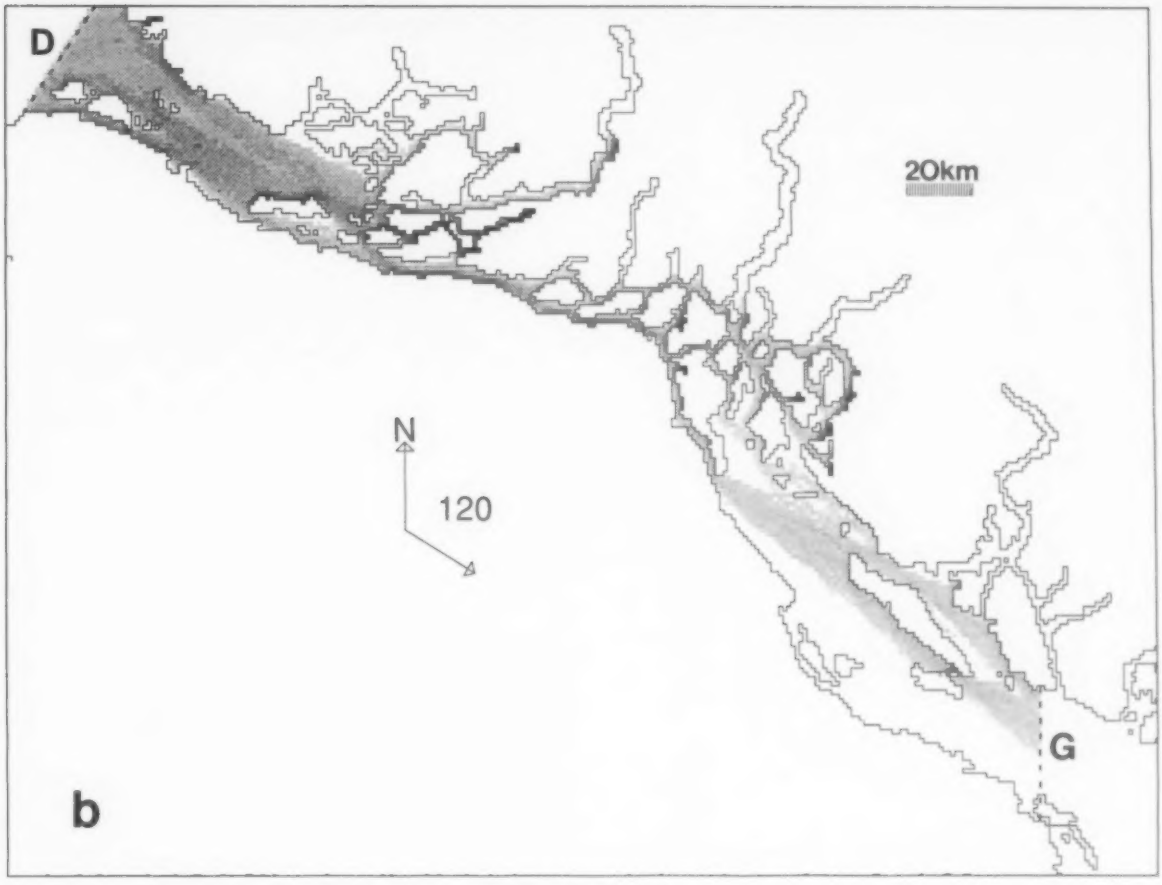

FIG. 8. (*Concluded*)

minimal estimates of migration success (Saila and Shappy 1963; Quinn and Groot 1984). Indirect evidence, however, indicates that the fraction of the run not caught that reaches the Fraser River is high. Besides the Nimpkish River on northern Vancouver Island, there are no fishable sockeye populations on either the east coast of the island or the British Columbia mainland across from the Island. Extensive surveys do not find sockeye in the many salmon rivers in this area. Moreover, the evolution of commercial catches along the northern Vancouver Island straits shows a sharp increase to a maximum at the peak of the migration (mid-August), followed by a drastic reduction (end of September), suggesting that few salmon remain in the region (INPFC 1984). Additionally, rates of straying, i.e. proportion of fish reaching spawning grounds other than their natal site, estimated for some populations of sockeye salmon in British Columbia are very low (<1%; Quinn et al. 1987). All this information suggests that a high proportion of the fish (90% or even higher) would reach the Fraser River from the mouth of Queen Charlotte Strait, if there were no fishing and natural mortality. None of the Monte Carlo simulations for the different strategies yielded that many fish arriving to the goal for headings between 115 and 130° (shaded areas in Fig. 5a, 6a, and 7a).

Timing

Tagging studies provide good estimates of the timing of the migration, assuming that handling and tagging do not stress the fish sufficiently to delay migration. The median timing for fish released in upper Johnstone Strait to the mouth of the Fraser River was 10 d (estimated from Verhoeven and Davidoff 1962). A simple extrapolation over distance indicates an expected median timing from the departure point in Queen Charlotte Strait of 14 d. The *normal* strategy yielded unrealistically late timing for headings between 115 and 130° (shaded area in Fig. 5b), while the *inertial* and *escapist* strategies yielded realistic timings for the same heading intervals and for high directional precision (shaded areas in Fig. 6b and 7b).

Heading distributions

Quinn et al. (1989) observed that the distribution of sockeye headings in the structurally more complex northern route was bimodal, with a large mode in the general direction of the home river (124°) and a smaller mode in the opposite direction (304°). The distribution of headings dislayed by tracked fish in the less complex region of the Strait of Georgia was unimodal (117°). Particular combinations of preferred heading and directional precision in the simulations generated the same pattern of movements, with bimodal distributions of headings in the more complex section of the route and unimodal distributions in the simpler region (Fig. 10). Although the bimodality of these distributions is not as prominent as that observed for the tracked fish, this result suggests that what appears as the outcome of a particular type of orientation mechanism can indeed be generated by frequent responses to the coast.

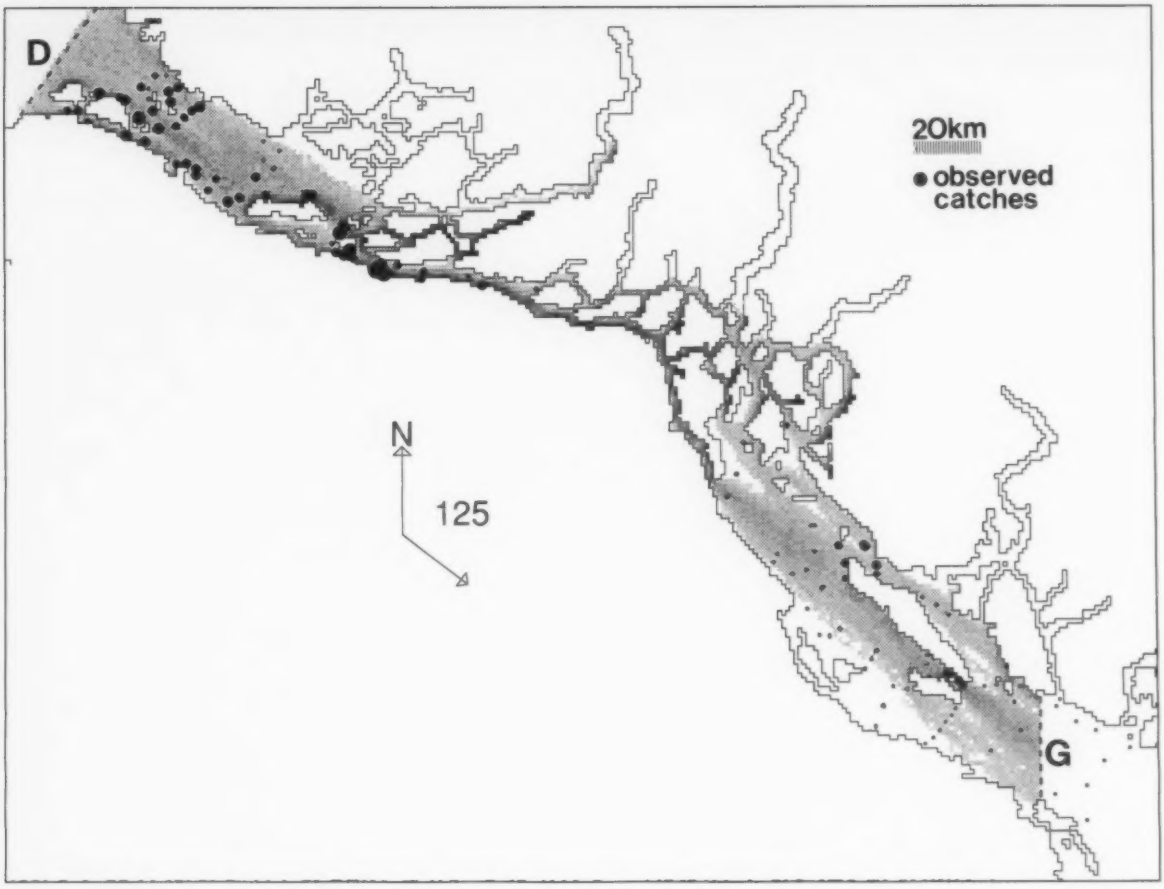

FIG. 9. Spatial distribution generated by 500 simulated fish for the *escapist* movement strategy for a preferred heading (μ) of 125° (shaded areas) and observed catch rates (●) in 1987 (Cooke et al. 1987) in logarithmic scale (D = departure line, G = goal).

Discussion

The movement strategies exhibited different degrees of realism in representing the actual movement behavior of sockeye salmon. The *normal* strategy failed to depict sockeye salmon movement satisfactorily, for it did not induce the fish to maintain its past trajectory. The *inertial* and *escapist* strategies succeeded in capturing the essence of observed movement patterns, but they failed to lead a realistic number of fish to the goal. All the models used ignore the weak correlation between fish and current direction and between fish speed and direction displayed by the tracked fish. These correlations could have increased the migratory efficiency of the fish. However, the movement models explicitly include directionality, which produces a much stronger bias in the home direction than these weak associations. The low efficiency shown by the simulated fish was due more to the tendency to be trapped in complex areas than by the lack of directional bias. Since this was not enough to explain the overall migratory success of Fraser River sockeye, it is concluded that the inclusion of an explicit correlation between fish and current direction or fish speed and direction would have not affected the results presented in a significant way.

The spatial distributions generated by the *inertial* and *escapist* movement strategies generally agree with that inferred from fishing survey data. However, neither fishing surveys nor ultrasonic tracking took place within the inlets along the northern coast, making the analysis incomplete. Indirect evidence suggests that there are few fish in these areas; although some of these areas are open to fishing, fishermen rarely visit them. This spatial pattern could be the result of the fishes' avoidance of specific areas, e.g. negative kinetic responses to water from rivers different than the home river. A behavior of this type would reduce the chances of the fish being lost in the many inlets characterizing this region, therefore increasing the proportion of fish getting to the goal. Consequently, it would decrease the time of passage.

The observed spatial distribution might also reflect learning as part of the migratory behavior (Dodson 1988). After spending some time trapped in a particular area, the fish could change the movement decision rules attempting to escape. Except for the addition of the escapement mechanism in the *escapist* strategy, the models considered do not include locally variable behavior or learning. Thus it appears that some form of directional orientation is necessary to explain the observed migratory behavior. However, such orientation alone is not sufficient, and additional responses (innate or learned) are required to explain the rapid migration through the complex regions.

In spite of the failure of these simple movement models to explain the migratory success of sockeye salmon, they consti-

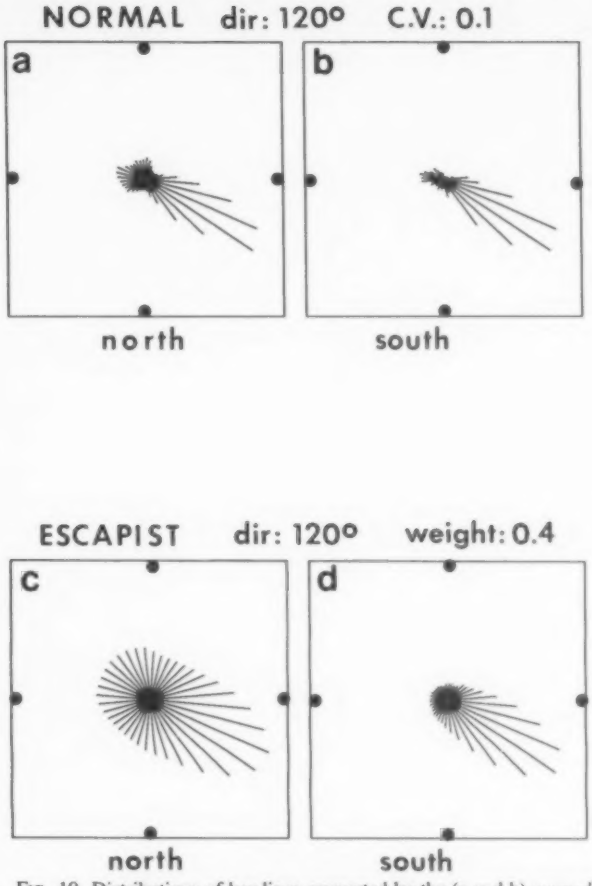

FIG. 10. Distributions of headings generated by the (a and b) *normal* and (c and d) *escapist* movement strategies for the Queen Charlotte – Johnstone Strait region (north) and for the Strait of Georgia region (south).

tute a useful tool for the exploration of theories to define migration mechanisms. The precision with which salmon are able to return to their home area and the precise timing associated with this return led to the early assumption that a precise course was required (Hartt 1966). The development of tracking techniques allowed for a direct evaluation of the trajectories and showed that movement was more complex than originally thought. The observed spread of critical choices by the fish has been attributed to the uncertainty intrinsically associated to their orienting ability (Leggett 1977, 1984). This idea was also supported by pioneer simulation models (Saila and Shappy 1963; Patten 1964), which suggested that even imprecise orientation was sufficient to guarantee realistic probability of return. The results of the present simulations suggest that the maintenance of constant heading for fish migrating through unfamiliar and structurally complex regions is more effective when some wandering is associated with the movement behavior.

There were differences in the observed movement patterns of sockeye salmon on the northern route to the Fraser River associated with two clearly defined areas. The Queen Charlotte and Johnstone straits are characterized by intricate geography and by tenuous influence of Fraser River waters; sockeye in this area exhibited a bimodal distribution of headings (Quinn et al. 1989). The Strait of Georgia is less intricate and has a stronger influence of Fraser River water; fish movement in this area was characterized by a unimodal distribution of headings.

Bimodal distributions of headings are characteristic of animals orienting to stimuli that give ambiguous information about "forward" and "backward" (e.g. the plane of polarized light; Taylor and Adler 1973). The bimodality observed for sockeye salmon headings could be explained by a similar mechanism (Quinn et al. 1989). The unimodal distribution of headings in the last part of the coastal migration could result from a decrease in the uncertainty about the "correct" direction as the fish detect olfactory cues from homestream waters. However, the simulation results suggest that the observed pattern of sockeye movement can occur even if the fish behavior rules are the same in the different regions; bimodal heading distributions were generated as a result of the more frequent interactions with the coast in the structurally more complex area.

The way movement behavior is conceptualized is the most important part of the modelling process. The type of model that we selected for salmon movement is one among several alternatives (see Saila and Shappy 1963; Okubo 1980; Stoddard et al. 1983). The selection of a specific type of model depends on the type of question that motivated its development and on the nature of the system under study. On the other hand, it is subordinated to the amount and detail of available information about the migration process. Probabilistic discrete step models, such as that used in this work, allow one to directly incorporate the specific and rich information about individual movements coming from tracking studies.

Acknowledgements

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Population and Community Patterns of Invertebrate Drift in an Unregulated Coastal Plain River[1]

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Benke, A. C., K. A. Parsons, and S. M. Dhar. 1991. Population and community patterns of invertebrate drift in an unregulated Coastal Plain river. Can. J. Fish. Aquat. Sci. 48: 811–823.

Drifting invertebrates were sampled monthly during postdusk hours for 2 yr in the Ogeechee River, a sixth-order river in the southeastern United States. Drift quantities were among the highest reported in the literature, with mean biomass varying from 2.41 to 2.46 mg dry mass/m^3 between years and mean density from 20.4 to 22.8 individuals/m^3. Major contributors to drift biomass were Ephemeroptera (30.3%), Coleoptera (25.1%), Plecoptera (16.6%), and Trichoptera (14.5%). Taxon-specific seasonal patterns of drift biomass for several mayflies (Ephemerellidae and *Isonychia*) and the dominant stonefly (*Perlesta placida*) resulted in biomass peaks in winter – early spring. Caddisflies (mostly Hydropsychidae and *Chimarra*) and beetles (Elmidae and Gyrinidae) complemented the mayfly–stonefly pattern with highest values in late spring – summer. These seasonal patterns coincided with standing stock biomass patterns on submerged wood (snags), their preferred habitat. Drift values were about 5.7 times higher in the Ogeechee than in another Coastal Plain river having only one fifth the amount of snags, suggesting a relationship between habitat abundance and drift. Percentages of snag-dwelling insects found in drift were substantially higher (0.1 to >1%) than is generally found for smaller streams, indicating drift distances and times much greater than previously shown.

Pendant 2 ans, on a prélevé des échantillons d'invertébrés à la dérive tous les mois après la tombée du jour, dans l'Ogeechee, une rivière de sixième ordre du sud-est des États-Unis. Les valeurs mesurées se rangent parmi les plus élevées qu'on ait signalées; ainsi, la biomasse moyenne à l'état sec varie de 2,41 à 2,46 mg/m^3 d'une année à l'autre et la densité moyenne, de 20,4 à 22,8 organismes/m^3. La biomasse à la dérive se composait principalement des organismes suivants : éphéméroptères (30,3 %), coléoptères (25,1 %), plécoptères (16,6 %) et trichoptères (14,5 %). En raison de variations saisonnières particulières à certains taxons de la biomasse à la dérive, notamment plusieurs éphéméroptères (éphémérellidés et *Isonychia*) ainsi que le principal plécoptère (*Perlesta placida*), il y a eu des pointes de production en hiver et au début du printemps. Les trichoptères (pour la plupart des hydropsychidés et *Chimarra*) et les coléoptères (elmidés et gyrinidés) complètent le tableau avec des pointes à la fin du printemps et en été. Ces variations saisonnières coïncidaient avec celles de la biomasse vivante du bois submergé (troncs d'arbres), habitat de prédilection de ces organismes. La biomasse des organismes à la dérive était environ 5,7 fois plus élevée dans l'Ogeechee que dans une autre rivière de la plaine côtière où il n'y qu'un cinquième de bois submergé, signe qu'il pourrait y avoir une relation entre l'abondance de l'habitat et l'importance de la biomasse à la dérive. La proportion d'insectes vivant dans les troncs d'arbre submergés qu'on a retrouvée dans la biomasse à la dérive était nettement plus élevée (de 0,1 à > 1 %) que ce qui s'observe généralement dans les cours d'eau de moindre importance, ce qui indique que la distance et le temps de dérive sont beaucoup plus élevés qu'on ne l'avait cru auparavant.

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The occurrence of benthic invertebrates drifting in the water column of streams is a well-studied phenomenon, but its ecological significance remains a puzzle in many respects (e.g. Waters 1972; Bournaud and Thibault 1973; Müller 1974; Statzner et al. 1984; Brittain and Eikeland 1988). After more than three decades of research on drift, two general types of questions have been raised: (1) What environmental factors or behavioral traits cause organisms that obtain food and shelter from their benthic environment to suddenly enter the water column for an uncertain fate? and (2) What is the magnitude and significance of their downstream transport for population, community, and ecosystem dynamics? The present paper deals with the latter, examining 2 yr of temporal patterns of drifting invertebrates within the context of total community dynamics in an unregulated Coastal Plain river.

In spite of many quantitative analyses of drift patterns, the drift literature is quite narrow in several respects. On one hand, many studies provide a detailed assessment of only a few species, giving a population perspective, but contribute little to our understanding of community dynamics. On the other hand, studies examining community patterns typically deal with the order/family level and provide little information on individual populations. Furthermore, drift studies are usually of only 1 yr duration (or less), and knowledge of annual variation is lacking.

From a geographical perspective, most drift studies have dealt with small streams (<5 m^3/s discharge), having moderate to high gradients, in cold temperate zones. Studies of medium to large rivers (i.e. >30 m^3/s) are scarce (see summary by Cellot 1989), and most of these are on regulated or otherwise modified systems. Indeed, in the contiguous United States, there are only about 42 reasonably natural rivers >200 km in length that possess no major dams or channel modifications (Benke 1990). Thus, the possibilities for studying invertebrate

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population and drift dynamics in undisturbed rivers of the United States and other industrialized countries are limited by the few that remain.

A substantial fraction of the remaining unregulated rivers in the contiguous United States are low-gradient systems in the southeastern states (Benke 1990). Benke et al. (1986) studied drift in one of these, the Satilla River, located on the Georgia Coastal Plain. They established that much of the drifting invertebrate community originated from the submerged wood habitat, or snags, rather than the more typical benthic habitats. Furthermore, drift in the Satilla was somewhat higher than found in most small streams that represent the majority of the drift literature (see summaries by Armitage 1977; O'Hop and Wallace 1983; Cellot 1989).

The present study was conducted on the Ogeechee River, another free-flowing river in Georgia, only two river basins north of the Satilla. Our objectives were to (1) describe how the temporal drift patterns of specific taxonomic groups (mostly at the generic level) create patterns at higher taxonomic and functional levels (i.e. order and community), (2) compare the magnitude of drift density and biomass in the Ogeechee with drift values from the Satilla River and the rest of the literature, (3) determine the consistency of population and community patterns of drift between years, and (4) determine the fraction of benthic animals that are found in the drift at a given point in time, considering its implications for distance travelled and the role of drift in population dynamics.

Study Site

The Ogeechee River is a low-gradient (0.02%) sixth-order river with 95% of its drainage located in the Coastal Plain of the southeastern United States. Mean annual discharge for the Ogeechee (47 yr) is 66.8 m^3/s, with 1982 being a relatively dry year (50.7 m^3/s) and 1983 relatively wet (79.1 m^3/s) (U.S. Geological Survey 1984; Benke and Parsons 1990). The mean channel width is about 33 m, with mean channel depth usually ranging from <1 to 4 m in a typical year (Benke and Meyer 1988). The channel meanders within a broad floodplain swamp which becomes inundated during high water.

Mean annual water temperatures were relatively high in 1982 and 1983 (19.5 and 19.2°C) compared with the long-term mean of 18.5°C (Benke and Meyer 1988; Benke and Parsons 1990). Temperatures typically exceed 25°C for extended periods during summer months, and sometimes drop below 10°C for short periods (e.g. 1–2 wk) during the winter.

Snags are a major invertebrate habitat in the Ogeechee, as they were in the Satilla, but are about 5 times more abundant (Wallace and Benke 1984). Virtually all the Trichoptera, Ephemeroptera, Plecoptera, Megaloptera, and Simuliidae are found on snags, as well as a substantial fraction of Coleoptera and Chironomidae. True benthic habitats, consisting mostly of shifting sand, are dominated by chironomids, oligochaetes, coleopterans, and molluscs (primarily *Corbicula fluminea*, which was absent from the Satilla).

Materials and Methods

Drift samples were taken with a Miller high-speed plankton net (Kahl Scientific Instruments, El Cajon, CA). It consists of a tubular fiberglass body (60 cm long, 89.4-cm^2 opening) attached to a net (90 cm long) which terminates in a PVC bucket (234-μm mesh). A propeller-type flowmeter (General Oceanics, model 2030) was installed inside the tubular body to determine the total volume filtered. Two samplers were attached to a framework of metal poles and positioned in the water from an anchored boat in midstream to avoid any bias associated with sampling too close to snags along the bank. Samples were collected for 2 h, beginning soon after dusk. Samples were collected at this time because in most streams, drift density increases dramatically at dusk and continues to be high throughout the night (e.g. Water 1972; Benke et al. 1986). During high water (>2 m depth), one net was positioned close to the surface and the other within 0.5 m of the bottom. During low water, both nets were arranged at middepth, about 1 m apart. Benke et al. (1986) showed that drifting invertebrates are well mixed in these Coastal Plain rivers and two samples should generally provide 95% CI that are 50% of the mean when densities are >0.1/m^3. Depending on current velocity, our procedure resulted in the filtration of 10–40 m^3 of water and collection of several hundred animals per net. Samples were collected at approximately monthly intervals from December 1981 to November 1983.

Invertebrates were usually identified to genus (in some cases, species), counted, and measured (head width or body length). Lengths were converted to individual dry mass (DM), using taxon-specific length–mass relationships (A. C. Benke, unpubl. data). We have chosen to present most of our temporal patterns in units of biomass rather than number of individuals, since biomass is a better reflection of production, food available to predators, and contribution to seston. Furthermore, biomass estimates are less dependent on mesh size than numerical estimates for most macroinvertebrate groups. Hereafter, drift biomass will mean biomass per volume of water (e.g. milligrams per 100 m^3), and drift density will mean number of individuals per volume of water.

Quantitative benthic and snag samples were collected within a few days of drift samples in order to determine the distribution of invertebrate secondary production. Although production analyses are reported elsewhere (e.g. Benke and Parsons 1990), we use the unpublished snag densities here to calculate the percentages of animals that are found in the drift at a moment in time during the postdusk interval. From 20 (1982) to 10 (1983) snag samples were analyzed on each sampling date (general procedure described in Benke et al. 1984). From these snag densities (number per square metre of snag surface) and biomass, we were able to calculate number per square metre and milligrams per square metre of channel bottom from equations that predict snag availability at various inundation levels (Wallace and Benke 1984). We multiplied these channel bottom densities by the mean channel width (33 m) to obtain the number of animals per metre length of river. Drift values (number per 100 m^3 and milligrams per 100 m^3) were also converted to number or biomass per metre length of river using discharge (U.S. Geological Survey 1984) and mean velocity (Roberts et al. 1985), i.e. number per second = number per cubic metre × cubic metres per second and number per metre = number per second ÷ metres per second. The ratio of the drift values to the snag values (both in units of number per metre) approximates the percentage of animals present in the drift.

Results

Monthly Patterns of Major Taxa

Ephemeroptera

Mayflies were one of the major drift components, with Baetidae (primarily *Baetis* spp.), Ephemerellidae (*Ephemerella*

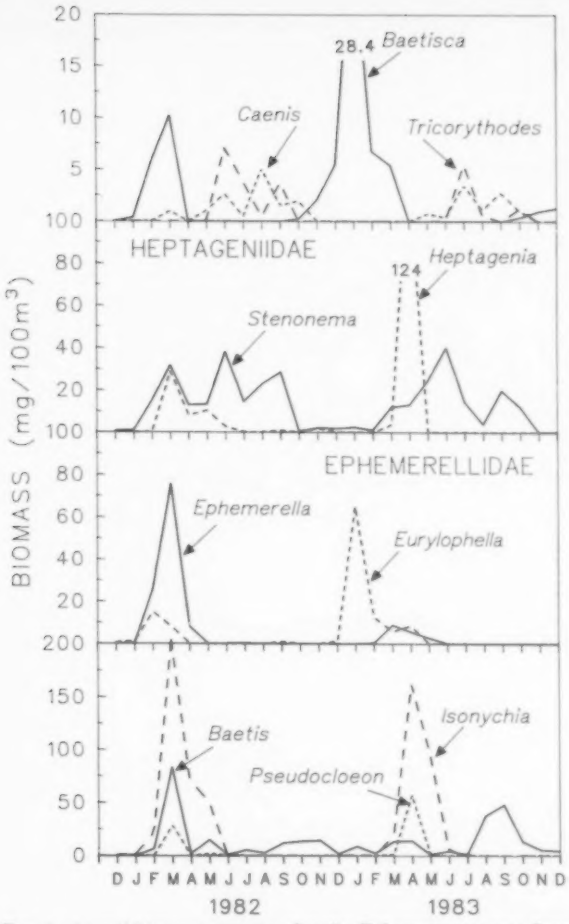

FIG. 1. Annual biomass patterns of major Ephemeroptera taxa found in postdusk drift in the Ogeechee River.

spp. and *Eurylophella* sp.), Heptageniidae (primarily *Stenonema* spp.), and *Isonychia* spp. as major contributors to both drift density and drift biomass (Fig. 1; Table 1). *Caenis* spp. and *Tricorythodes* sp. were numerically abundant (Table 1), but contributed little to biomass (note smaller scale in Fig. 1). Mean annual drift densities and biomass for most taxa were remarkably consistent between years (Table 1) even though mean discharge was 55% higher in the second year.

With the exception of *Baetis* spp. and *Stenonema* spp., most mayfly taxa were strongly seasonal, as shown by their consistent temporal patterns during two consecutive years (Fig. 1). *Isonychia* spp., with the highest drift biomass of any mayfly, primarily drifted during late winter and early spring, the only times when they occurred in great abundance on snags (Jacobi 1988; D. I. Jacobi and A. C. Benke, unpubl. manuscr.). Similarly, drifting Ephemerellidae (*Ephemerella* spp. and *Eurylophella* sp.) were found primarily during winter when they were most common on snags, a pattern similar to that found in the Satilla River (Benke et al. 1979). Clearly, strong winter generations were responsible for the drift pattern of these three genera. *Pseudocloeon* sp. and *Baetisca* sp. also appeared to have winter–spring drift activity, but low numbers in drift or on snags were inconclusive in this regard. *Heptagenia* sp. drift biomass was highest in the spring, near the end of a winter cohort, although they were present on snags throughout the year (D. I. Jacobi and A. C. Benke, unpubl. manuscr.).

Stenonema spp. and *Baetis* spp. both drifted throughout the year with fairly high densities and biomass (Fig. 1; Table 1), and they were consistently numerous on the snag habitat as well (Jacobi 1988; D. I. Jacobi and A. C. Benke, unpubl. manuscr.). Unlike the winter generation species which were mostly univoltine, *Stenonema* and *Baetis* included two to three coexisting species each, with rapid growth and several generations per year (Benke and Jacobi 1986). Only *Caenis* spp. (Caenidae) and *Tricorythodes* sp. (Tricorythidae), two relatively small mayflies, had strictly summer periods of drift (Fig. 1), coinciding with their occurrence on snags.

Trichoptera

The caddisflies were comparable in terms of drift abundance with the mayflies, and they were well represented throughout the year. Two families of net-spinning taxa, the Hydropsychidae (*Cheumatopsyche* spp. and *Hydropsyche* spp.) and Philopotamidae (*Chimarra moselyi*), constituted the major portion of caddisfly density and biomass (Fig. 2; Table 1). The Leptoceridae (especially *Nectopsyche* sp. and *Oecetis* sp.) were major contributors to density, but not to biomass. Mean densities of most caddisfly taxa were relatively consistent between years, except for *Oecetis* which increased their densities by sevenfold in the second year.

It was difficult to discern seasonal patterns among the caddisflies, although *Chimarra moselyi* and *Cheumatopsyche* (primarily *pasella*) appeared to have their highest drift biomass in the warmer months (Fig. 2). The data suggest two or three peaks of *Cheumatopsyche* each year (late winter, late spring, and late summer). All caddisflies were found on the snag habitat throughout most of the year, with *Cheumatopsyche*, *Hydropsyche*, and *Chimarra* having the highest biomass and production and at least two generations per year (A. C. Benke, unpubl. data).

Coleoptera

Drift biomass of beetles (larvae plus adults) was second only to mayflies, although their densities were less than half of either the mayflies or caddisflies (Table 1). The Elmidae (especially *Stenelmis* spp. and *Dubiraphia* sp.) and Gyrinidae (mostly *Dineutus* sp.) were the major drift components (Fig. 3; Table 1). Both adults and larvae of the elmids were abundant, but adult gyrinids were rarely found in drift nets. Density and biomass of each major taxon were relatively consistent between years (Table 1).

Adults and larvae of elmids were most common during the spring and summer. Gyrinid larvae were most prevalent from early spring to early summer (Fig. 3). These beetles were very abundant on snags throughout most of the year, but lower densities were also found in benthic habitats (A. C. Benke, unpubl. data).

Plecoptera

Perlesta placida (Perlidae) was the major component of stonefly biomass for both years and had the highest mean biomass of any invertebrate species (Table 1). However, its presence was consistently limited to late winter and early spring (Fig. 4), when it was also common on the snag habitat (A. C. Benke, unpubl. data). No seasonal biomass patterns were apparent for several relatively large perlid stoneflies with low drift densities (*Perlinella* sp., *Paragnetina kansensis*, and *Neoperla clymene*). *Pteronarcys dorsata* (Pteronarcyidae) and *Tae-*

TABLE 1. Mean annual drift density (numbers and biomass) and percentage of animals (from the snag habitat only) in the drift during postdusk sampling for 1982 and 1983 in the Ogeechee River, Georgia. Percentages were estimated only for those taxa that exclusively inhabit snags and also have a minimum mean drift density of 10/100 m^3. Species and genera in parentheses indicate the major taxon within the genus or family, respectively.

	Number				Biomass			
	1982		1983		1982		1983	
	No./100 m^3	%	No./100 m^3	%	mg/100 m^3	%	mg/100 m^3	%
Ephemeroptera								
Baetidae (*Baetis*)	94.3	0.7	114.2	0.5	14.5	1.2	18.0	1.6
Ephemerellidae (*Ephemerella* spp.)	32.7	0.6	40.8	1.9	10.6	1.9	9.2	0.3
Isonychia spp.	50.1	2.5	35.6	3.8	26.9	1.7	23.8	10.8
Heptageniidae (*Stenonema* spp.)	70.3	0.6	48.4	0.8	18.2	1.5	22.6	3.8
Caenis spp.	19.8	1.3	26.9	3.3	1.0	2.6	0.8	1.8
Tricorythodes sp.	19.2	0.3	21.9	0.1	1.2	0.6	0.6	0.03
Total	286.4	0.8	287.8	0.7	72.4	1.5	75.0	1.6
Trichoptera								
Cheumatopsyche(pasella)	74.6	0.3	45.1	0.1	17.4	0.3	9.2	0.1
Hydropsyche (rossi)	9.7	0.1	20.0	0.02	5.3	0.1	6.5	0.02
Nectopsyche spp.	11.2	3.7	24.9	3.0	2.6	6.8	5.1	4.1
Oecetis spp.	59.7	23.7	456.0	21.3	1.0	5.0	2.8	3.6
Triaenodes sp.	1.7	—	4.3	—	0.4	—	0.6	—
Chimarra moselyi	57.2	0.1	19.2	0.03	15.7	0.2	4.2	0.1
Total	214.1	0.3	569.5	0.3	42.4	0.2	28.3	0.05
Coleoptera adult								
Stenelmis spp.	18.7	—	25.8	—	8.7	—	12.3	—
Dubiraphia sp.	19.4	—	17.1	—	8.5	—	7.8	—
Gyrinidae.	0.1	—	0.2	—	0.3	—	0.5	—
Other	2.2	—	2.2	—	2.2	—	1.0	—
Total	40.4	—	45.3	—	19.6	—	21.7	—
Coleoptera larvae								
Stenelmis spp.	51.4	—	32.1	—	14.4	—	7.3	—
Dubiraphia sp.	3.6	—	10.5	—	1.0	—	2.9	—
Gyrinidae (*Dineutus*)	10.9	—	5.5	—	17.2	—	31.6	—
Other	9.0	—	3.8	—	5.0	—	1.3	—
Total	74.9	—	51.9	—	37.6	—	43.1	—
Plecoptera								
Perlesta placida	44.2	3.5	43.8	8.3	24.8	3.5	42.0	19.1
Paragnetina kansensis	1.2	—	0.1	—	0.5	—	0.004	—
Neoperla clymene	0.7	—	1.3	—	0.5	—	0.6	—
Perlinella sp.	8.3	—	7.0	—	1.3	—	1.9	—
Taeniopteryx sp.	90.7	7.9	9.5	2.9	2.1	1.4	0.4	0.8
Pteronarcys dorsata	0.3	—	0.5	—	0.6	—	2.8	—
Other	37.8	0.5	50.8	0.6	2.6	0.8	1.1	3.3
Total	183.2	2.0	113.1	1.1	32.2	0.7	48.8	1.6
Simuliidae								
Simulium spp.	46.0	0.2	40.3	0.3	1.5	0.1	1.6	0.5
Chironomidae								
Tanytarsini	102.4	—	55.0	—	2.1	—	1.1	—
Cricotopus spp.	92.2	—	139.0	—	2.8	—	8.2	—
Tanypodinae	170.0	—	80.6	—	9.3	—	3.4	—
Polypedilum spp.	36.6	—	71.6	—	1.4	—	2.4	—
Other	48.8	—	38.0	—	3.2	—	1.7	—
Total	450.0	—	384.2	—	18.8	—	16.8	—
Other Diptera								
Ceratopogonidae	8.5	—	9.2	—	1.3	—	0.65	—
Chaoboridae	4.2	—	2.1	—	0.4	—	0.5	—
Total	12.7	—	11.3	—	1.7	—	1.15	—

TABLE 1. (*Concluded*)

	Number				Biomass			
	1982		1983		1982		1983	
	No./100 m³	%	No./100 m³	%	mg/100 m³	%	mg/100 m³	%
Crustacea								
Amphipoda								
(*Hyalella azteca*)	10.9	—	28.2	—	0.4	—	1.1	—
Isopoda								
(*Lirceus lineatus*)	11.0	—	9.6	—	0.8	—	0.5	—
Cladocera	118.6	—	302.9	—	0.7	—	1.1	—
Copepoda	450.4	—	307.2	—	2.6	—	1.6	—
Ostracoda	2.6	—	8.4	—	0.04	—	0.7	—
Total	593.5	—	656.3	—	4.54	—	5.0	—
Odonata and Megaloptera								
Anisoptera	15.3	—	7.0	—	9.9	—	5.4	—
Zygoptera	13.9	—	1.9	—	0.8	—	0.2	—
Megaloptera								
(*Corydalus cornutus*)	0.3	—	0.3	—	1.5	—	0.02	—
Total	29.5	—	9.2	—	12.2	—	5.6	—
Miscellaneous								
Climacia sp.	1.9	—	3.3	—	—	—	—	—
Oligochaeta	51.4	—	17.0	—	—	—	—	—
Mollusca	10.2	—	5.1	—	—	—	—	—
Hydracarina	61.1	—	94.5	—	—	—	—	—
Total	124.6	—	119.9	—	—	—	—	—
Grand total	2042.6	—	2277.5	—	241.3	—	245.7	—

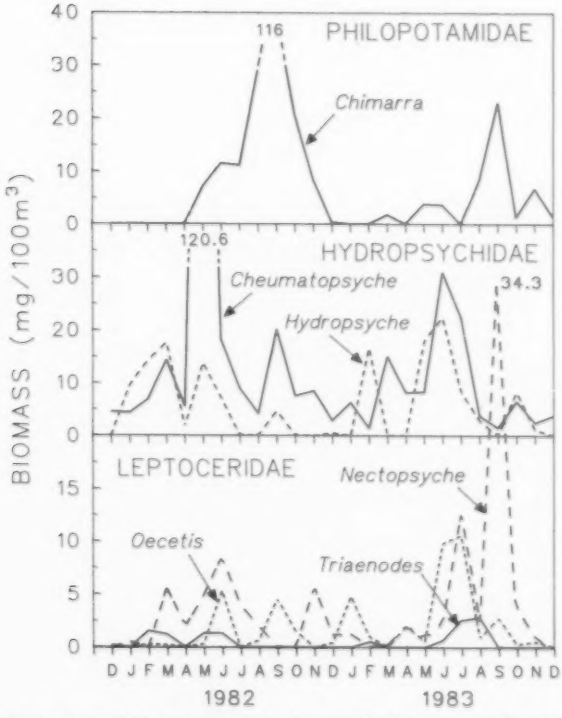

FIG. 2. Annual biomass patterns of major Trichoptera taxa found in postdusk drift in the Ogeechee River.

niopteryx sp. (Taeniopterygidae), the major detritivorous stoneflies in the Ogeechee, were also found primarily during cool months (Fig. 4). *Taeniopteryx* had a relatively high density (0.9/m³) in 1982 due to an extremely high density of early instars on a single date.

Diptera

Dipterans were second only to the crustaceans in density, but their biomass was usually no more than half any of the four orders discussed above (Table 1). Chironomidae were by far the most abundant dipteran family, and the many taxa originated from snags as well as main channel and backwater benthic habitats (Benke et al. 1986). Members of the Tanypodinae and *Cricotopus* group (several species of *Cricotopus* and closely related genera) were the most abundant chironomids (Fig. 5; Table 1), with *Polypedilum* spp. and Tanytarsini (mostly *Rheotanytarsus*) also common. Biomass fluctuated greatly throughout the year for most of these multivoltine and multiple-species populations, and it was difficult to discern any seasonal trends.

The other major dipterans were Ceratopogonidae, Simuliidae, and *Chaoborus* spp. Although simuliids were not among the most abundant dipterans in the drift, they appeared to have their highest abundance in winter and late summer, coinciding with a bimodal pattern of black fly production on the snag habitat (Benke and Parsons 1990). None of the other dipteran taxa exhibited any notable seasonal patterns.

Crustaceans

Crustaceans (primarily microcrustaceans) had the highest drift densities (>6/m³) of any major invertebrate group, yet their biomass was about an order of magnitude lower than the other major groups (Fig. 6; Table 1). The larger isopods (*Asel-*

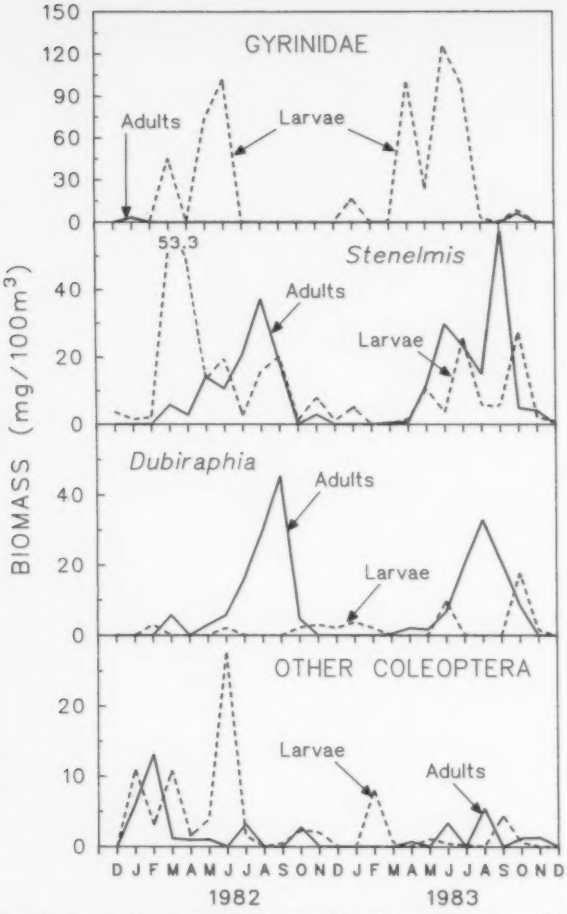

FIG. 3. Annual biomass patterns of major Coleoptera taxa found in postdusk drift in the Ogeechee River.

lus forbesi and *Lirceus lineatus*) and amphipods (*Hyalella azteca*) were fairly common on several dates, but generally low in density. Isopods were more abundant during cool months and amphipods during warm months. Among the microcrustaceans, copepods were most abundant, with their biomass as high as most of the dipteran taxa. Copepod biomass showed relatively little variability throughout the year, usually fluctuating between 1 and 5 mg/100 m^3 (Fig. 6). Cladocerans were also common throughout the year, but biomass fluctuated from almost zero to >8 mg/100 m^3. Cladoceran densities were higher in the second year whereas copepods were somewhat lower, the net result being very similar crustacean densities between years. Ostracods were found in abundance on only a single date.

Monthly Patterns and Magnitude of Major Invertebrate Groups

The Ephemeroptera and Plecoptera were among the highest groups in drift biomass, and both orders clearly peaked during late winter – early spring (Fig. 7). The mayfly pattern was dominated by the winter-active ephemerellids and *Isonychia* and the stoneflies by *Perlesta placida*. Biomass of drifting mayflies was as high as 4–5 mg/m^3 and stoneflies >2 mg/m^3 during early spring. The annual biomass patterns for Trichoptera and

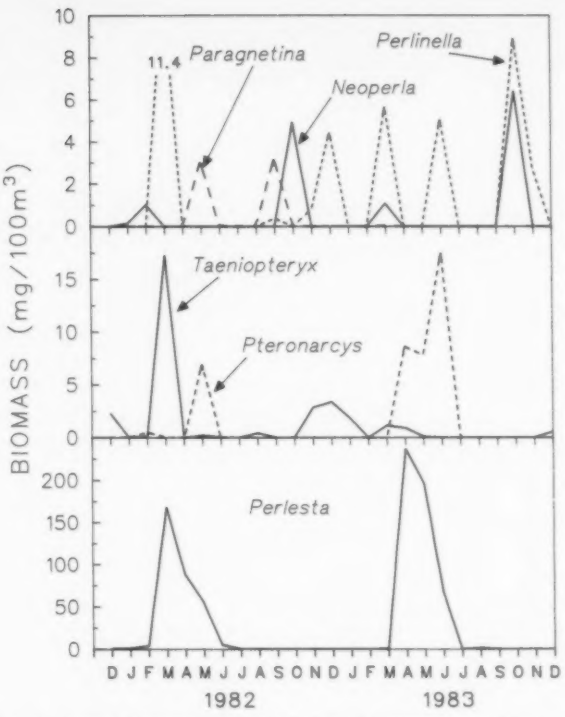

FIG. 4. Annual biomass patterns of major Plecoptera taxa found in postdusk drift in the Ogeechee River.

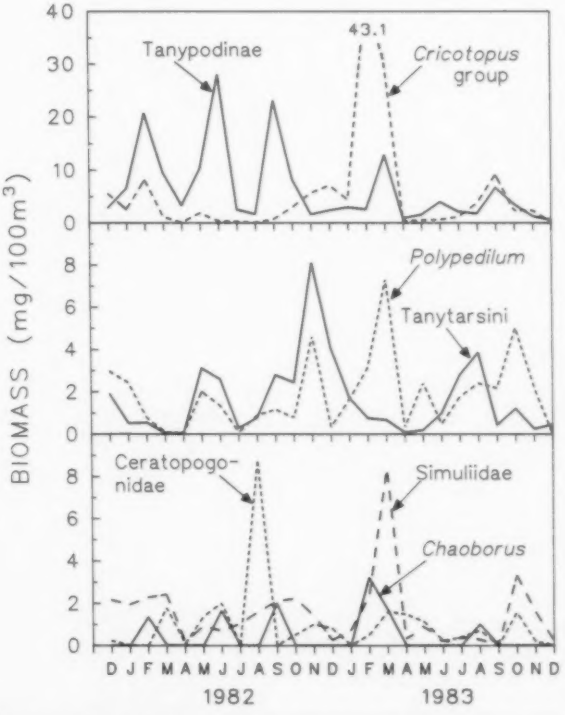

FIG. 5. Annual biomass patterns of major Diptera taxa found in postdusk drift in the Ogeechee River.

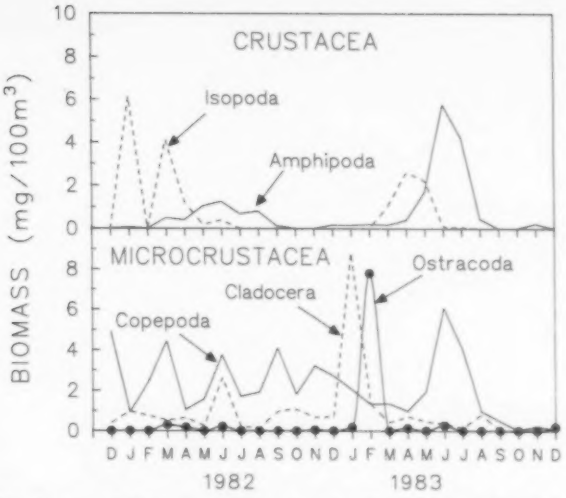

FIG. 6. Annual biomass patterns of major Crustacea taxa found in postdusk drift in the Ogeechee River.

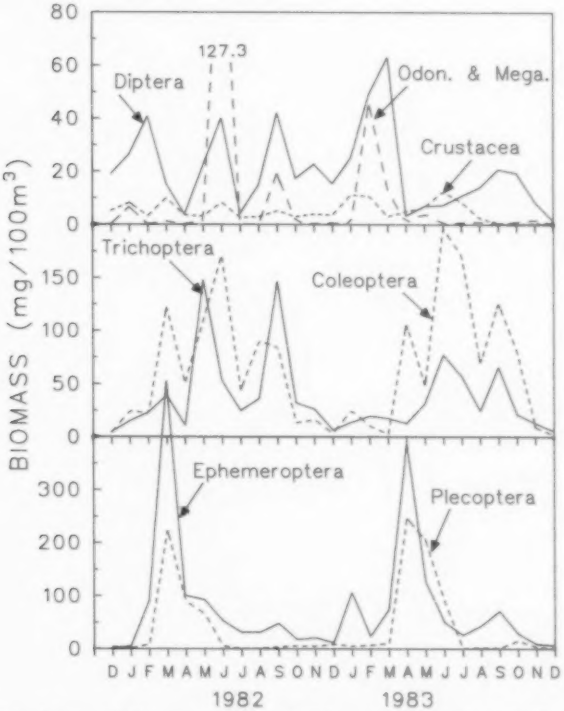

FIG. 7. Annual biomass patterns of major groups (mostly orders) of invertebrates found in postdusk drift in the Ogeechee River. Odon. = Odonata, Mega. = Megaloptera.

Coleoptera tended to complement that seen for stoneflies and mayflies. Biomass of caddisflies and beetles was highest during the warmer months, with two or three peaks per year, often exceeding 1 mg/m³ (Fig. 7). The caddisfly and beetle patterns were not so much dominated by individual taxa as with the mayflies and stoneflies, but each represented more of a composite of several species that were generally more abundant at higher temperatures.

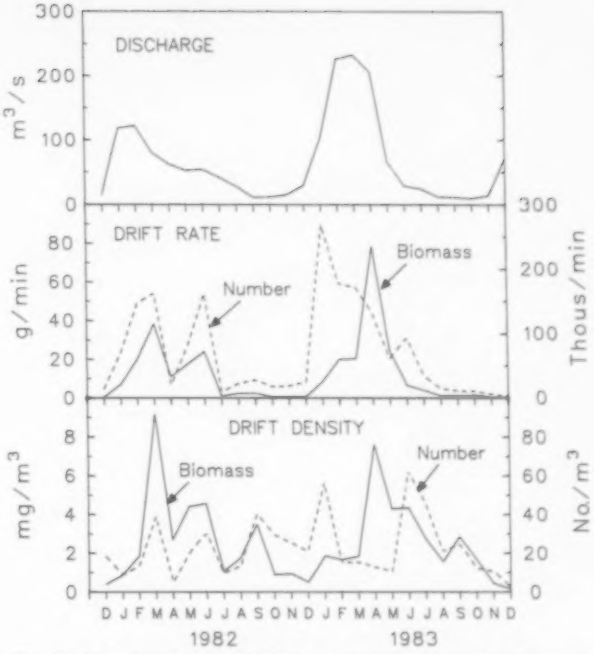

FIG. 8. Annual patterns of drift rate and drift density (number and biomass) for total invertebrate drift from postdusk samples in the Ogeechee River. Also shown is mean monthly discharge.

Falling well below the four major insect orders in drift biomass were the Diptera, Crustacea, and the remaining large predators (besides the stonefilies). Among these, the dipterans were several times higher than the crustaceans in their drifting biomass (Table 1), and neither group was found to have a seasonal pattern (Fig. 7). The crustaceans had a relatively low variability throughout the year whereas the dipterans as a group fluctuated greatly. The large predators (Odonata and Megaloptera) were relatively uncommon in the drift, but on occasion their combined drifting biomass was comparable with the dipterans and crustaceans (Fig. 7).

If all invertebrate taxa are combined, the highest biomass was found in late winter – spring, a pattern strongly influenced by the winter-active mayflies and stoneflies (Fig. 8). A secondary peak occurs in late summer, primarily due to contributions from the Trichoptera and Coleoptera. Throughout the year, drift biomass usually fluctuated between only 1 and 9 mg DM/m³ and averaged about 2.4 mg/m³ for both years (Table 1). The seasonal biomass patterns were not reflected in any recognizable pattern of numerical density (Fig. 8). However, the variation in density was not great, usually ranging from 10 to 60/m³ across all dates. As with biomass, mean densities were almost identical between years (20.4 and 22.8/m³; Table 1).

Multiple regression analyses were performed in which biomass (milligrams per cubic metre) of major drift groups was the dependent variable and discharge and temperature were independent variables (Table 2). Trichoptera and Coleoptera showed a significant positive relationship with temperature, reflecting their higher drift patterns during warm months, but only the beetles had a relatively high r^2 (0.48). The Diptera were the only group to show a significant relationship to discharge. Neither the Ephemeroptera nor Plecoptera had a significant relationship with temperature or discharge in spite of the strong seasonal pattern of these orders. Total drift biomass

TABLE 2. Significance levels from multiple regression analyses using drift biomass of major groups as dependent variables and discharge and water temperature as independent variables. ns = not significant.

	Discharge	Temperature	r^2
Ephemeroptera	ns	ns	—
Plecoptera	ns	ns	—
Crustacea	ns	ns	—
Trichoptera	ns	$p < 0.05$	0.23
Coleoptera	ns	$p < 0.01$	0.48
Diptera	$p < 0.05$	ns	0.28
Total biomass	$p < 0.05$	$p < 0.05$	0.29

was significantly related to both discharge and temperature, but r^2 was only 0.29. There was not a significant relationship between these independent variables and total drift density.

Total drift rates (the product of drift density or drift biomass and discharge, sensu Waters 1969) showed strong seasonal patterns, since discharge is characteristically highest during winter and spring (Fig. 8). Peaks in numerical drift rates (particularly in 1983) coincided with the rise in discharge during early winter whereas peaks in biomass drift rates occurred when mean monthly discharge was declining. The increase in numerical drift rate may reflect a higher fraction of the population entering the drift (see below) and increased survival of newly recruited animals. As the water rises, inundating additional snag habitat, a higher absolute number of new recruits can survive within a greater habitat space. Life history analyses indicate that recruitment (egg hatching) of black flies (Benke and Parsons 1990) and mayflies and stoneflies (A. C. Benke, unpubl. data) is particularly high as water levels rise during the early winter. The lag in biomass peak appears to reflect the individual growth that occurs during the high-water periods. The precipitous decline of biomass in spring appears to be due to emergence (particularly mayflies and stoneflies, A. C. Benke, unpubl. data) as well as a diminishing discharge.

Percentages of Drifting Invertebrates

Using the drift densities (number per cubic metre) and benthic densities (number per square metre) and converting each to number per metre length of river, we calculated the percentages of several populations found in the drift at a given moment in time. Our analyses were limited to those invertebrate taxa (mostly genera) that occurred in relatively high abundance in the drift and that were found almost exclusively on the snag habitat during quantitative sampling of various habitats. We only included taxa which had a drift density of at least 10/100 m^3 for both years to help reduce the possibility of sampling artifacts. Taxa that also occurred in other habitats (such as chironomids and beetles in the sandy benthic habitat) were not included in this analysis.

Both the Plecoptera and Ephemeroptera had extremely high percentages of animals drifting at night, whether one considers either numbers or biomass (Table 1). The mean values for percent drifting were slightly >1% of numbers for Plecoptera and <1% for Ephemeroptera, but values were sometimes as high as 10% and as low as 0.1% (Fig. 9). Percent drifting for both the Trichoptera and Simuliidae was considerably lower (usually 0.1–0.3%), but again the temporal variability was typically about two orders of magnitude. Temporal patterns were difficult to discern, but Ephemeroptera, Plecoptera, and Simuliidae showed some of their highest percentages drifting in winter–spring.

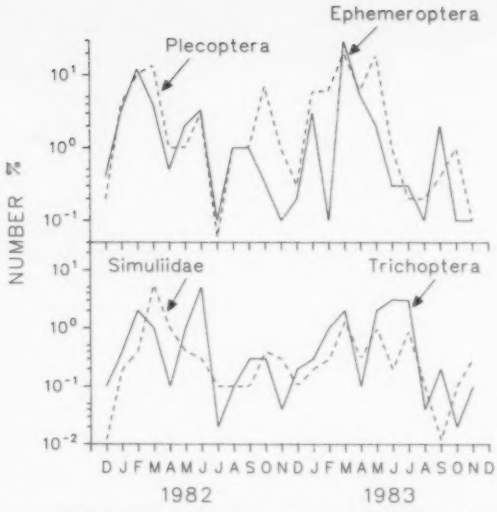

FIG. 9. Annual patterns showing the percentages of the most abundant snag-dwelling taxa drifting during postdusk sampling. Drift densities (no/m^3) and benthic densities (no./m^2) were first converted to no./m of river length (see text) from which percentages were calculated.

Discussion

Invertebrate drift density and biomass in the Ogeechee River were among the highest ever reported for lotic systems and were strongly dependent on organisms from the snag habitat. Drift patterns of most major genera were very seasonal, and complementary patterns of genera within a given order resulted in substantial drift for most orders throughout the year. Nonetheless, seasonal patterns of dominant genera (e.g. *Isonychia* and *Perlesta*) played a major role in shaping both order and community-level patterns. The net result was that drift biomass peaked in later winter–spring but remained relatively high throughout the year. Furthermore, drift biomass patterns for most genera and families and for the entire invertebrate community were similar for two consecutive years, suggesting a high level of community stability. Comparison of the drift density and biomass with standing stock of these same taxa from the snag habitat shows that an extremely high fraction of the population is found in the drift during the night.

Ogeechee–Satilla Comparisons

It is of considerable interest to compare the drift patterns and magnitudes from the Ogeechee with earlier results from the Satilla (Benke et al. 1986) because these rivers (1) show strong physical and chemical similarities, (2) are among the few remaining rivers in the contiguous 48 states without major man-made alterations (Benke 1990), and (3) may represent the only free-flowing streams of this size on which detailed drift analyses have been conducted. The consistent patterns and magnitude of drift between consecutive years (1982 and 1983) in the Ogeechee suggest that our data are reasonably representative for this river. Furthermore, Benke et al.'s (1986) drift data for the Satilla also appear to be representative of this system, since densities in 1975 were not substantially different from those found in 1974 (Coomer et al. 1978) and 1976 (Benke et al. 1979).

Total drift density and biomass in the Ogeechee (21/m^3 and 2.4 mg DM/m^3) were much higher than in the Satilla (3.2/m^3

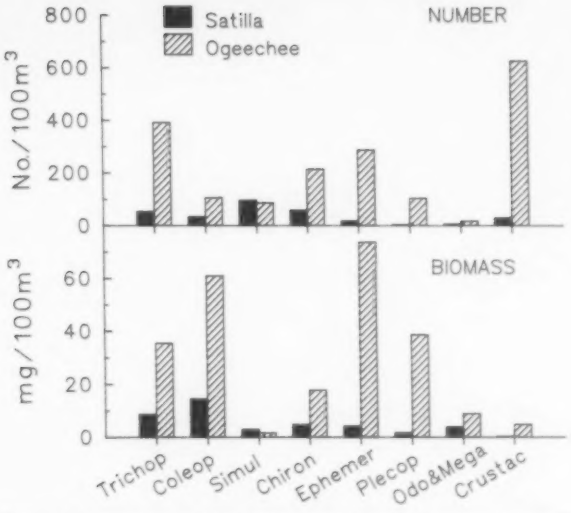

FIG. 10. Comparison of drift densities and biomass between the Ogeechee River (mean for 1982 and 1983) and Satilla River (mean of two sites for 1975; Benke et al. 1986).

and 0.43 mg DM/m^3). This was true of most major invertebrate groups, but particularly for the mayflies (Fig. 10). The latter difference can be partly attributed to a more diverse mayfly community with much higher production per snag surface area in the Ogeechee (Jacobi 1988) than was found in the Satilla (Benke et al. 1984). Only for the simuliids were drift density and biomass higher in the Satilla, a reflection of substantially higher black fly production (per unit surface area of snags) (Benke et al. 1984; Benke and Parsons 1990). In spite of major differences in drift magnitude, the remaining components of these invertebrate communities were very similar in taxonomic composition, particularly with regard to the predominance of net-spinning caddisflies and elmid beetles during summer months.

Aside from production differences among certain taxa between the rivers (e.g. the mayflies), the higher drift densities in the Ogeechee can be attributed to (1) a difference in net mesh size and (2) a true difference caused by habitat availability. A smaller mesh size in the Ogeechee (234 versus 400 μm in the Satilla) enhanced our ability to capture small invertebrates (e.g. chironomids and microcrustaceans), but was unlikely to have greatly affected drift biomass, since biomass of most populations is contained within the later instars.

We hypothesize that the major reason for differences in drift density and biomass between the rivers is the amount of snag habitat available for colonization. Benke et al. (1986) showed that about 80% of the drift biomass and 76% of the density originated from the snag habitat in the Satilla. Using the same criteria for habitat assignment as Benke et al. (1986), we conservatively estimate that about 76% of the drift biomass in the Ogeechee originates from the snags, but only about 46% of the density (largely due to high numbers of microcrustaceans and chironomids in the Ogeechee). Since snag surface area was approximately 5 times higher in the Ogeechee than in the Satilla (Wallace and Benke 1984), we might expect roughly 5 times more drift biomass (assuming that production per snag surface area is similar in the two rivers). In fact, mean drift biomass in the Ogeechee (1982–83) was about 5.7 times higher than found in the Satilla (1975).

Magnitude of Drift — General Comparisons

The abundance of invertebrates drifting in the Ogeechee River is among the highest reported for either small streams or large rivers, with means of 21 individuals/m^3 and 2.4 mg DM/m^3 and maxima as high as 60/m^3 in June 1983 and 9 mg/m^3 in March 1982. Although higher drift densities have sometimes been reported during peak drift periods (e.g. Allan 1987), densities in most lotic systems are more typically 0.5–5.0/m^3 and 0.2–1.0 mg/m^3 (see summaries in Armitage 1977; O'Hop and Wallace 1983; Cellot 1989), ranges within which Satilla values fall (Benke et al. 1986). In general, the few values reported for rivers with a mean discharge >30 m^3/s are on the low end of this range (see summary in Cellot 1989). On the other hand, recent estimates on the Mississippi River were somewhat higher, ranging from 3 to 11/m^3 (Scheaffer and Nickum 1986; Koetsier and Bryan 1989). At the upper extreme are drift densities as high as 3000/m^3 in the Kootenai River following a major reduction in discharge below a dam (Perry and Perry 1986). Unfortunately, except for the Ogeechee and Satilla, all large rivers on which drift densities have been estimated are strongly regulated or have been otherwise modified by man. It is difficult to know what drift densities and patterns might have been in their unaltered state.

In addition to total community density and biomass, there are several taxon-specific aspects of our drift data worth mentioning. Our total mayfly mean density of about 2.9/m^3 is high compared with most of the drift literature, but higher values have been found in some streams (e.g. Clifford 1972; Allan 1982, 1987; Smith-Cuffney and Wallace 1987). *Baetis* spp. are probably the most-studied of any drifting insect, and although our mean density of about 1/m^3 was less than some estimates (e.g. Pearson and Franklin 1968; Clifford 1972; Ciborowski and Clifford 1983), it was higher than most. For example, *Baetis* and *Stenonema* were the two most abundant drifting mayflies in two other southeastern streams (Cowell and Carew 1976; Stoneburner and Smock 1979), but their densities were substantially lower than in the Ogeechee. Ephemerellids and *Isonychia* have both been found in previous drift studies (e.g. Cloud and Stewart 1974; Stewart and Szczytko 1983; Ciborowski and Clifford 1983), but unlike the Ogeechee, they have usually been reported as summer active. Our ephemerellid drift densities (mean = 0.3–0.4/m^3, >1/m^3 in winter) are relatively high by most standards, although maximum values >10/m^3 have been reported (Ciborowski and Clifford 1983; Haney et al. 1983). Our mean drift densities for *Isonychia* (0.35–0.5/m^3) are higher than previously found (e.g. Cloud and Stewart 1974; Eckblad et al. 1984; Scheaffer and Nickum 1986). *Caenis* and *Tricorythodes* were both reported to be summer drifters by Cloud and Stewart (1974), as we found in the Ogeechee, but with densities somewhat less than our own.

Trichoptera are common constituents of the drift in most streams, although they often have lower drift densities than other orders. Our estimate of 5.7/m^3 for mean Trichoptera drift density in 1983 (Table 1) exceeds previous estimates for this order. Only Pearson and Kramer's (1969) short-term estimate for *Oligophlebodes* is comparable. Our hydropsychid drift densities (>0.8/m^3 in 1982) are considerably higher than most previous estimates for this family (e.g. Cloud and Stewart 1974; Cowell and Carew 1976; Stoneburner and Smock 1979), although McLay (1968) and Scheaffer and Nickum (1986) reported densities >1/m^3. Previous studies agree with our

results showing that hydropsychids have their highest drift during warm months.

The high drift density of beetles (mostly elmids) in the Ogeechee River (1.0–1.2/m^3) is very unusual (e.g. Brittain and Eikeland 1988), but is similar to findings from the Satilla River (Benke et al. 1986). The abundance of elmids in the drift and on snags in these two rivers suggests that their occurrence is characteristic of Coastal Plain streams (see also Cowell and Carew 1976).

Stoneflies are common drift components in many streams, but their drift densities are usually not especially high (e.g. Stewart and Szczytko 1983). Our plecopteran drift estimates are among the highest reported (1–2/m^3, primarily *Perlesta placida*), with Allan (1987) and Smith-Cuffney and Wallace (1987) providing similar estimates.

It is now well established that microcrustaceans are important natural components of a wide range of unregulated lotic systems from small streams (e.g. Clifford 1972; O'Doherty 1985; Shiozawa 1986; Brown et al. 1989) to large rivers (e.g. Saunders and Lewis 1988). They may originate from the main channel of first- to fifth-order streams (Brown et al. 1989), from drainage of marshy areas into small streams (Clifford 1972), or from extensive flooding of large river flood plains (Saunders and Lewis 1988). Unlike most drift components in the Ogeechee, drifting crustaceans appear to be flushed from the floodplain swamp, where they are found in great abundance (A. C. Benke, unpubl. data), at medium to high discharge. At low discharge, they probably originate as "leakage" from backwater areas. Drift density of microcrustaceans is strongly dependent on mesh size, making comparisons among systems difficult. Our densities (6/m^3) were reasonably high for a mesh size of 240 μm, but they were not nearly as high as "zooplankton" densities found by Saunders and Lewis (1988) using a plankton net (35 μm) in the unregulated Apure River of western Venezuela.

Factors Affecting Community Drift Patterns

Understanding the community drift dynamics of invertebrates in the Ogeechee River is a matter of understanding how the specific patterns of species and genera combine to create patterns at the ordinal level and how the ordinal patterns combine to create the community pattern. Attempting to understand community drift dynamics without understanding the dynamics of its component taxa can lead to erroneous conclusions about relationships with environmental variables such as temperature and discharge.

Some studies have shown a relationship between drift and various environmental variables such as discharge, current, temperature, dissolved oxygen, sediment export, and benthic densities (e.g. Pearson and Franklin 1968; Cowell and Carew 1976; O'Hop and Wallace 1983). Although we found that total drift biomass in the Ogeechee had a significant relationship with temperature and discharge, it would be wrong to conclude that these factors have a strong effect on drift patterns. Their correlation with drift biomass was low ($r^2 = 0.29$), and there was no relationship between these two variables and drift density. Furthermore, the temporal biomass patterns of the entire community (Fig. 8) are strongly influenced by winter mayflies and stoneflies (Fig. 7), neither of which are correlated with discharge or temperature (Table 2). If high discharge occurred in late summer or fall, drift from these taxa would not increase, since they are scarce at this time of year.

Only the Trichoptera and Coleoptera showed a significant positive relationship with temperature. It is difficult to know whether this is simply a matter of seasonal abundance on snags or a greater propensity to drift during warmer temperatures. However, examination of Fig. 9 shows that the percentage of Trichoptera drifting was at least as high in the winter as in the summer, suggesting that the temperature relationship simply reflects abundance on snags. The only group having a significant positive correlation with discharge was the Diptera. This may seem counterintuitive, since one might expect high discharge to dilute drift density, but this relationship supports the idea that midges with short generation times (Stites and Benke 1989) are able to track the discharge through reproduction and colonization of new snag substrates as they become inundated.

Various workers have noted that in northern regions, drift reaches maximum values during warm months and minima during the winter (e.g. Brittain and Eikeland 1988). As more studies have been conducted in southerly latitudes, attempts have been made to draw generalities which relate seasonal patterns to latitude (e.g. Stoneburner and Smock 1979; Koetsier and Bryan 1989). Our data show that while individual species or genera may have strong and predictable annual patterns of drift, one cannot easily generalize about the pattern of drift for an entire invertebrate community. The annual drift pattern of a given system will depend strongly on the relative abundances of individual taxa and their taxon-specific life histories. For example, the Ogeechee drift biomass would have been highest in summer had certain winter-active mayflies and stoneflies been absent or low in abundance. This is what occurred in the Satilla where *Isonychia* spp. were absent and ephemerellids and *Perlesta placida* were less common than in the Ogeechee (Benke et al. 1986).

Drift as a Factor in Population Dynamics

The percentages of invertebrate populations found in the postdusk drift of the Ogeechee River (typically from 0.1 to 10%) are somewhat higher than found in the Satilla River (Benke et al. 1986) and much higher than has been found in small streams (i.e. often <0.01%; Waters 1972; Brittain and Eikeland 1988). A consistent pattern found in the Ogeechee and Satilla was that among the four groups that are almost exclusively snag dwellers, the percentages of mayflies and stoneflies were several times higher than for the caddisflies and black flies (Table 1). The lower fraction of caddisflies and black flies drifting is consistent with the fact that most snag-dwelling caddisflies live within retreats or nets (Hydropsychidae and Philopotamidae), and black flies are firmly attached to the substratum by their posterior ring of hooks and salivary secretions. Mayflies and stoneflies are apparently more easily dislodged by the current as they forage for food across the snag surface. It would be interesting to know whether mayflies and stoneflies, which are more active swimmers in the drift (Otto and Sjostrom 1986), have a higher probability of returning to snags than do caddisflies and black flies. The extremely high drift percentage of >20% for *Oecetis* in both years seems anomalous (but see Benke et al. 1986), possibly the result of not adequately sampling their preferred habitat (i.e. they occurred in another habitat or were not effectively collected from snags). However, *Oecetis* spp. are able to swim (e.g. Wiggins 1977), and their occurrence in the drift may reflect such behavior.

The general concept of drifting animals is that they are disassociated from their substrate (actively or passively) and are car-

TABLE 3. Three scenarios illustrating different possible drift distances and drift times, assuming that 1% of the population is found in the nocturnal drift at any moment. Distance and time depend on the percentage of the population that drifts during the course of the night (not the same percentage as that drifting at any moment).

% of population drifting per night	Mean distance travelled (km)	Mean time in drift (h)
1	18	10
10	1.8	1
100	0.18	0.1

ried in the current for short distances (<10 m) in a short amount of time (<1 min) (e.g. Waters 1972; Statzner et al. 1984). Return to the substrate is usually viewed as a simple matter of "settling" (e.g. McLay 1970; Elliott 1971; Allan and Feifarek 1989). In Coastal Plain rivers, returning from drift to a snag habitat concentrated along the bank is not so simple. Once swept into the main current, the return of invertebrates to preferred habitat is dictated primarily by hydrodynamics. Settling to the bottom only takes them to an inhospitable sandy habitat. Thus, drift in these Coastal Plain rivers, or any large river whose optimal habitat is widely distributed in patches, is likely to travel much longer distances than has been shown to occur in small streams.

Benke et al. (1986) have illustrated that if 0.1% of the population is in the nocturnal drift at a moment in time, current velocity is 0.5 m/s, and drift occurs for only 10 h of darkness per day, individuals are likely to travel between 180 m (if 10% of the population is involved per day) and 1.8 km (if 1% is involved). Using a higher estimate of 1% of the population in the drift at one time (close to most values in the Ogeechee; Table 1), we can project three scenarios for drift distances and times (Table 3). If only 1% of the population drifts throughout the night (i.e. the same individuals as at any given moment), they would travel 18 km. At the other extreme, if 100% of the population was involved in nocturnal drift each night, the average individual would still travel 180 m in the current. Regardless of which scenario is most realistic, there would be a net displacement of 100% of the population downstream a distance of 18 km in 100 d. Even though these are rough approximations, they illustrate that drift is a major phenomenon for invertebrate populations in these rivers and that drift distances are normally much longer than previously envisioned.

In view of the extremely high percentages drifting, it would appear that populations with long development times (e.g. >1 yr) might be depleted over the course of a year, a problem that has been extensively discussed in the early drift literature (e.g. Müller 1974). However, short development times of many species (e.g. Benke and Jacobi 1986; Hauer and Benke 1987; Stites and Benke 1989) help explain why depletion might not be as extensive as one might think (e.g. Benke et al. 1986). Even most univoltine species in the Ogeechee (e.g. *Perlesta placida* and *Ephemerella* spp.) are fast-growing species that have larval development times of 6 mo or less and long periods of inactivity (e.g. dormant egg stage).

Fate of Drift and Contribution to Seston

Once in the current, away from the snag substrate, one of two things is most likely to happen to a drifting animal. It will intercept a snag upon which it might colonize, or it will be eaten by a predator. Van Arsdall (1977) found that artificial snags were rapidly colonized from the drift in the Satilla River, and Cellot (1989) even estimated drift rate by colonization of artificial substrates in the Rhone. On the other hand, if drifting animals have not successfully intercepted a snag by dawn, with nocturnal densities of more than 20/m^3 (mixed sizes), they would appear to offer an attractive food source for insectivorous fishes. Many fishes rely heavily on drifting invertebrates (e.g. Brittain and Eikeland 1988), and this is undoubtedly true for rivers like the Ogeechee and Satilla as well (Benke et al. 1985). However, the fraction of drifting animals which successfully recolonize snags and how rapidly fish predators are able to decimate the residual drift at dawn are both interesting and unanswered questions.

Many lotic invertebrates are specialized as filter-feeders to take advantage of the particulate organic matter in transport (i.e. seston) of which drift generally represents some unknown fraction. Whether drift is an important nutritional component for filter-feeders depends on two things: (1) the proportion of seston which consists of drift and (2) the selectivity of the filter-feeder. Wallace et al. (1987) analyzed seston on five sample dates from the Ogeechee River and estimated that animals constitute about 0.6% of the seston. Our current analyses which include many more drift samples, much larger volumes of water filtered, and more direct estimates of biomass indicate that the animal contribution is somewhat lower. With a mean drift biomass of 2.4 mg DM/m^3 (Table 1) and a mean seston value of 1.1 g ash-free dry mass/m^3 (Wallace et al. 1987), we obtain an animal fraction of 0.2%. This low fraction is consistent with the relatively few studies that have estimated both organic seston and animal drift, with drift generally contributing <1% to the seston (e.g. Naiman 1983; O'Hop and Wallace 1983). Although animals represent a small fraction of seston biomass, late instars of *Hydropsyche* spp. and *Cheumatopsyche* spp. consumed from 27 to 71% animal matter, contributing from 68 to 92% of their production (Wallace et al. 1987). Thus, the animal fraction of the seston is very important, sufficient as a food source for certain macrofiltering invertebrates and potentially for the fish community as well (Benke et al. 1985).

Conclusions

Our study suggests that in medium-sized (and possibly large) low-gradient rivers, relatively unaltered by man, drift densities and biomass are likely to be substantially higher than found in most small (< 5 m^3/s) streams. Unfortunately, most river drift studies are on regulated or otherwise altered systems, where drift densities are sometimes relatively low (e.g. Cellot 1989) but may be extremely high such as below dams (e.g. Perry and Perry 1986). The consistency of drift patterns and magnitude in the Ogeechee River for two consecutive years suggests a higher degree of stability in invertebrate community dynamics than we might otherwise expect in an environment that fluctuates greatly throughout the year and between years. The temporal patterns of community biomass for a particular system appear to be linked to the relative abundance of seasonal taxa such as *Isonychia* spp., rather than being a function of latitude, temperature, or discharge. In rivers like the Ogeechee and Satilla, where the snag habitat occurs primarily along the banks, and the shifting sandy bottom is not conducive to upstream migration of most taxa, drift is the only means of exit from a desiccated or overcrowded habitat and, aside from egg-hatching, the only means of colonization on a newly inundated habitat. The generality of our results can only be examined if

comprehensive drift studies are conducted in additional unregulated natural rivers.

Acknowledgments

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Feeding of Atlantic Cod (*Gadus morhua*) at Low Temperatures

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Waiwood, K. G., S. J. Smith, and M. R. Petersen. 1991. Feeding of Atlantic cod (*Gadus morhua*) at low temperatures. Can. J. Fish. Aquat. Sci. 48: 824–831.

Satiation level, feeding frequency and maximum meal size of Atlantic cod (*Gadus morhua*) fed frozen shrimp (*Pandalus montagui*) were determined at temperatures of 1, 4, and 8°C. Satiation level was predicted by a statistical model which separated the occurrence of feeding from the amount ingested. Decreased consumption of food at low temperatures was found to be primarily a function of decreased feeding frequency rather than decreased meal size. On a daily basis, cod ate 87, 77, and 54% of the time on average at 8, 4, and 1°C, respectively. The average meal size, calculated over feeding days only, was directly related to the size of the fish and not to temperature. However, the maximum meal size was smaller, particularly for the larger fish at low temperatures.

On a déterminé le niveau de satiété, la fréquence d'alimentation et la consommation maximale de nourriture par repas en étudiant des morues de l'Atlantique (*Gadus morhua*) nourries de crevettes (*Pandalus montagui*) à des températures de 1, 4, et 8°C. On a prévu le niveau de satiété au moyen d'un modèle statistique permettant de séparer l'occurrence de l'ingestion de nourriture de la quantité ingérée. On a constaté que la baisse de la consommation de nourriture à basse température est fonction principalement de la baisse de la fréquence d'alimentation plutôt que de la diminution de la consommation. On a déterminé qu'en moyenne, la morue mange chaque jour 87, 77 et 54 % du temps à 8, 4 et 1°C respectivement. La quantité moyenne de nourriture consommée en un repas, calculée d'après les jours d'alimentation seulement, est directement reliée à la taille du poisson et n'a aucun lien avec la température. Toutefois, on a constaté que la consommation maximale par repas est plus petite et ce, en particulier dans le cas des poissons de grande taille, à basse température.

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Although most Atlantic cod (*Gadus morhua*) stocks spend a significant period of their annual cycle at temperatures below 3°C (Bratberg and Hylen 1964; Templeman and Fleming 1965; Woodhead and Woodhead 1965; Nakken and Raknes 1987) and have been observed to feed at temperatures below 0°C (Lee 1952; Templeman and Fleming 1965), few studies have considered the effect of low temperature on feeding. Temperature has been shown to affect several feeding-related factors in fish including digestion rates (Brett and Higgs 1970; Jobling et al. 1977), appetite (Grove et al. 1978; Jobling 1988; Waiwood 1978), preferred food particle size (McKenzie 1938), satiation time (Grove et al. 1978), and feeding frequency and maximum meal size (Gwyther and Grove 1981). However, few of these studies on cod have considered temperature effects below 4°C. Notable exceptions are studies by Tyler (1970) who studied gastric evacuation rates at temperatures as low as 2°C and Brown et al. (1989) who investigated feeding activity and growth of 0+ cod (0.5–6 g) over the range 0.6–8.3°C.

Studies on low-temperature feeding in cod are essential to our understanding of the biology of the species and of its potential exploitation through aquaculture. For example, the use of bioenergetic models (e.g. Kerr 1982) for cod require estimates of maximum ration (R_m) which reflect the feeding behaviour associated with thermal conditions that the cod seasonally experience. The parameter R_m relates to culture situations because fish are usually fed at this level to maximize growth. The ability to predict R_m over a wide range of temperatures is important in estimating seasonal feed requirements and to reduce environmental degradation and profit loss due to overfeeding.

This study was undertaken to characterize aspects of the feeding behaviour of cod over the temperature range 1–8°C. The effect of low temperature on feeding frequency, meal size, and maximum meal size are evaluated with the aid of a two-component feeding model which separates the frequency of feeding and the amount consumed when feeding occurred. Conservative estimates of R_m for use in models such as Kerr's (1982) are obtained here as functions of temperature and the size of the animal.

Materials and Methods

Experimental Procedures

Cod weighing 215–5552 g were collected by otter trawl from Passamaquoddy Bay and transported to the St. Andrews

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Biological Station, St. Andrews, New Brunswick. The fish were held in 5000-L circular tanks which were supplied with filtered seawater (27.8–31.5 ppt). The smaller fish were captured during the winter of 1984–85, while the larger fish had been in captivity for up to 4 yr. During the pre-experimental period (minimum of 3 wk), the cod were fed three times a week with a moist pellet food consisting of ground winter flounder, ground shrimp, commercial herring meal, and vitamins. With the exception of those fish to be tested at 8°C, the cod were held at ambient temperatures. Due to difficulties in acclimating cod to high temperatures during the winter, the fish used for the 8°C treatment were maintained at this temperature throughout the fall period. A natural photoperiod was used throughout the pre-experimental, acclimation, and experimental periods. All of the experiments were conducted between January and April 1985.

At the beginning of each experiment, individual fish were anaesthetized with tricaine methanesulfonate (MS-222), measured, weighed, tagged (Floy Tag Manufacturing, Seattle, WA, type FD68B), and randomly assigned to experimental tanks. Smaller fish (215–1500 g) were placed in seven circular tanks containing approximately 750 L of running aerated seawater. Temperature in the tanks was kept constant to within ±0.5° by the regulated addition of heated seawater. Depending on size, four to six fish were placed in each tank. Fish greater than 1500 g were placed in two to three 3200-L circular tanks (five to six per tank). Mean stocking densities (±1 SD) for the small and large tanks were 3.12 g/L (±1.1) and 5.00 g/L (±1.2), respectively. As the experiment progressed, any fish which appeared to be in poor health were discarded.

After introduction to the experimental tanks, the fish were allowed to recover from handling and to acclimate to the test conditions for 8–10 d. During this time, they were fed frozen shrimp (*Pandalus montagui*) once daily. To ensure high quality, the shrimp were collected at 1- to 2-wk intervals throughout the experimental period (January–February). For each batch, shrimp less than 2.5 g and greater than 4.5 g were removed, the average weight of 100 of the remaining shrimp was calculated, and the shrimp were frozen (−30°C). At feeding, thawed shrimp were placed in the tanks and the number of shrimp eaten by each fish was recorded until no feeding had occurred for at least 10 min. Uneaten shrimp were removed. The number of shrimp eaten by each fish multiplied by the average weight for the batch represented the weight of shrimp consumed. A combination of colouration, size, tag location, tag colour, and scars was used to identify individual fish and to keep track of the amount of food consumed by each fish.

Individual feeding was recorded for up to 38 d in some cases (Table 1). Fish were not reused in subsequent experiments. The experiment was conducted at 1, 4, and 8°C (nominal). In order to determine if maximum daily intake was achieved by feeding to satiation once a day, additional experiments were conducted at 8°C using twice-daily feedings (to satiation). It was assumed that if there were no significant differences between these feeding regimes at 8°C, the same would hold at lower temperatures where the rate of digestion was known to be much slower. Further details of the experimental conditions are given in Table 1. Five fish were removed from the experiment due to illness, etc., and therefore the numbers of fish given in the table refer to final totals for healthy animals only. Fish were weighed at the end of the experiment. However, accurate estimates of growth over the course of the experiments could not be made because fish were weighed prior to being acclimated but not at the beginning of the feeding experiments. This protocol was adopted to avoid any disturbance in feeding due to handling stress.

TABLE 1. Details of experimental conditions for the feeding experiment. Note that number of fish refers to the number of fish remaining at the end of the experiment.

Mean temperature (°C)	Number of fish	Feeding regime	Length of experiment (d)
0.77	4	Once daily	12
0.77	20	Once daily	17
1.30	8	Once daily	38
4.09	14	Once daily	24
4.09	14	Once daily	16
4.09	7	Once daily	10
7.81	41	Once daily	12
7.81	41	Twice daily	12

Statistical Models

An exploratory plot of the feeding data showed that the mean amount of food eaten per day by each fish and the associated variance were related. This relationship obviates the use of a normal probability model to test for the effects of temperature on feeding behaviour, since the mean and variance are assumed to be independent for this distribution. Transformation of the data by taking logarithms to stabilize the variance (e.g. Snedecor and Cochran 1967, p. 329) was considered to be inappropriate due to the presence of nonfeeding days. The substitution of a constant (e.g. 1 or 0.5) for no food eaten would be misleading because the proportion of nonfeeding days appeared to vary inversely with the temperature. That is, the transformed data would become more skewed or distorted at the lower temperatures.

The observation that the frequency of feeding days appears to be related to the temperature motivated the following approach. The events of feeding and nonfeeding were considered separately from how much was eaten when the cod did feed. This implies that any factor that may trigger feeding does so as a toggle between the condition of feeding and not feeding and not in an incremental sense from zero units of food to one unit of food. Therefore the feeding behaviour was modelled as a two-phase phenomenon. The first phase consisted of a model of the probability of either feeding or nonfeeding taking place, while the second phase dealt with the average amount eaten by each fish conditional on the event that feeding had occurred. Similar models are presented in Coe and Stern (1982) for the occurrence and amount of rainfall and in Pennington (1983) and Smith (1988) for the occurrence and amount of ichthyoplankton and fish, respectively.

In all of the above cases the event of whether or not something occurred or was present was modelled as a Bernoulli random variable. In our case the number of days that the ith fish fed during the n_i days the fish was observed was modelled as a sum of n_i Bernoulli random variables (feeding = 1 and nonfeeding = 0) with the probability of feeding occurring on any one day represented by P_i. That is, the number of feeding days was modelled by a binomial distribution with parameters n_i and P_i. The number of feeding days would be predicted by n_iP_i. Covariates (e.g. x_{ij} = initial weight of the ith fish for the jth temperature treatment) were related to the expected value ($E[\ ]$)

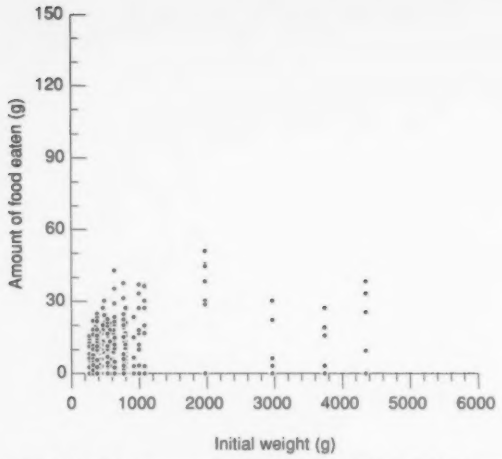

FIG. 1. Weight of shrimp eaten on each feeding day by each fish against the initial weight of each fish in the 1°C feeding experiment.

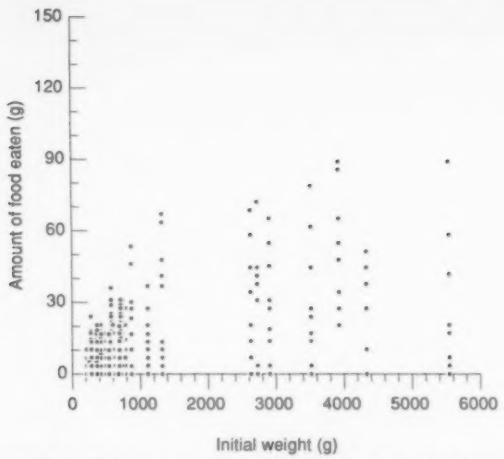

FIG. 2. Weight of shrimp eaten on each feeding day by each fish against the initial weight of each fish in the 4°C feeding experiment.

of the probability of feeding via the logit transformation (McCullagh and Nelder 1983) as

$$(1)\quad E\left[\log\left(\frac{\hat{P}_i}{1-\hat{P}_i}\right)\right] = \beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}.$$

The β are unknown coefficients which need to be estimated. Predictions from linear models of the form in equation (1) will give values in the range $(-\infty,\infty)$ and are therefore more appropriately related to the logit which is defined over the same range than to the P_i which are defined to be in the range [0,1].

Three kinds of probabilities of feeding were modelled for each fish. The first was simply the probability of feeding on any day t ($t=1,\ldots,n_i$), i.e. $P[(\text{feed})_t]$. This assumes that feeding on any one day was independent of what had occurred on the day before. The conditional events of the probability of feeding on day t given feeding or not feeding on day $t-1$, expressed as $P[(\text{feed})_t|(\text{feed})_{t-1}]$ or $P[(\text{feed})_t|(\text{not feed})_{t-1}]$, respectively, were also modelled. These latter probabilities were defined to investigate the possible dependence between the occurrence of feeding on day t and feeding or not feeding on day $t-1$.

The average amount of food eaten by the ith fish (y_i) for feeding days only was plotted against the standard deviation for each fish. The linear relationship between the mean and standard deviation indicated a constant coefficient of variation which is consistent with y_i exhibiting a gamma distribution. The expected variance to mean relationship for the gamma distribution is

$$V[y_i] = kE^2[y_i].$$

The gamma distribution provides a very flexible model for positive random variates in that it can accommodate frequency distributions ranging from highly skewed to symmetric in shape (McCullagh and Nelder 1983; Aitkin et al. 1989). Covariates were related to the average amount of food consumed on feeding days through an exponential function to ensure that predicted values were always positive, i.e.

$$(2)\quad E[y_i] = \exp\left(\beta_0 + \sum_{j=1}^{k} \beta_j x_{ij}\right).$$

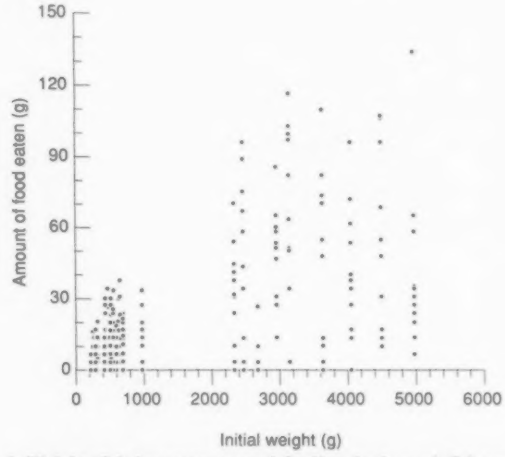

FIG. 3. Weight of shrimp eaten on each feeding day by each fish against the initial weight of each fish in the 8°C feeding experiment.

Parameter estimates were obtained using the Generalized Linear Interactive Modelling (GLIM) software (Payne 1985).

Results

Although the individual daily feeding patterns of the cod appeared to be quite variable, a number of general patterns emerged. At 8°C, feeding occurred on about 90% of the days on average and fish missed more than one consecutive day of feeding less than 1% of the time. At 4 and 1°C, respectively, the cod fed approximately 78 and 54% of the days and missed more than one consecutive feeding day an average of 5 and 31% of the time.

There was no apparent trend in the maximum meal size with temperature for fish with initial weights in the range of 200–1000 g (Fig. 1–3). However, for fish >1000 g the maximum meal size increased with increasing temperature.

The theory of generalized linear models refers to the measure of the discrepancy between the observations and the fitted values from a model, formed from the logarithm of the ratio of the respective likelihoods as *deviance* (McCullagh and Nelder

TABLE 2. Analysis of deviance for probability of eating on any day t. Variables defined as follows: μ = grand mean; Temp = temperature; Temp·Tank = experimental tanks nested within temperature; wt = initial weight; ln(wt) = natural logarithm of initial weight.

(a) Binomial error with logit link (scale = 1)

Model	First difference in deviance	Degrees of freedom	P level	Scale
μ				3.01
+ Temp	169.60	2	0.000	1.45
+ Temp·Tank	19.25	21	0.570	1.59
+ wt	0.56	1	0.452	1.46
+ ln(wt)	0.52	1	0.471	1.46
+ wt	2.04	1	0.153	3.02
+ ln(wt)	0.79	1	0.374	3.03

(b) Parameter estimates for final model: μ + Temp (scale = 1.10); T_j refers to the estimated mean logit at temperature j

Parameter	Estimate	Standard error
μ	0.161	0.925
$T_4 - T_1$	0.981	0.138
$T_8 - T_1$	1.78	0.176

TABLE 3. Analysis of deviance for probability of eating on day t given eating on day $t-1$. Variables defined as follows: μ = grand mean; Temp = temperature; Temp·Tank = experimental tanks nested within temperature; wt = initial weight; ln(wt) = natural logarithm of initial weight.

(a) Binomial error with logit link (scale = 1)

Model	First difference in deviance	Degrees of freedom	P level	Scale
μ				3.04
+ Temp	166.90	2	0.000	1.51
+ Temp·Tank	19.25	21	0.570	1.59
+ wt	0.02	1	0.888	1.52
+ ln(wt)	0.09	1	0.808	1.52
+ wt	4.81	1	0.283	3.02
+ ln(wt)	3.58	1	0.059	3.03

(b) Parameter estimates for final model: μ + Temp (scale = 1.08); T_j refers to the estimated mean logit at temperature j

Parameter	Estimate	Standard error
μ	−0.235	0.130
$T_4 - T_1$	1.297	0.180
$T_8 - T_1$	2.127	0.176

1983). The deviance is defined specific to the probability distribution being used for the response. Factors and/or covariates were included in the models discussed in the Materials and Methods section, according to whether or not a significant portion of the deviance was explained by these variables. The significance of the deviance explained by any one factor or covariate was assessed by a χ^2 test. The results of fitting the model in equation (1) for the three measures of feeding frequency are presented in Tables 2–4. The top section of these tables presents the analysis of deviance for these models. The order of fitting the covariates and factors is given sequentially. For example in Table 2a the grand mean, μ, is included into

TABLE 4. Analysis of deviance for probability of eating on day t given no eating on day $t-1$. Variables defined as follows: μ = grand mean; Temp = temperature; Temp·Tank = experimental tanks nested within temperature; wt = initial weight; ln(wt) = natural logarithm of initial weight.

(a) Binomial error with logit link (scale = 1)

Model	First difference in deviance	Degrees of freedom	P level	Scale
μ				1.46
+ Temp	45.18	2	0.000	0.99
+ Temp·Tank	29.78	21	0.096	0.87
+ wt	1.77	1	0.183	0.99
+ ln(wt)	2.65	1	0.104	0.98
+ wt	0.00	1	0.999	1.48
+ ln(wt)	0.47	1	0.493	1.47

(b) Parameter estimates for final model: μ + Temp (scale = 0.99); T_j refers to the estimated mean logit at temperature j

Parameter	Estimate	Standard error
μ	0.523	0.118
$T_4 - T_1$	1.146	0.244
$T_8 - T_1$	2.366	0.593

TABLE 5. Predicted unconditional and conditional probabilities of feeding on day t for the three temperatures in the cod feeding experiment.

	Temperature		
	1°C	4°C	8°C
$\hat{\Pr}[(\text{feed})_t]$	0.543	0.768	0.874
$\hat{\Pr}[(\text{feed})_t \mid (\text{feed})_{t-1}]$	0.435	0.756	0.869
$\hat{\Pr}[(\text{feed})_t \mid (\text{not feed})_{t-1}]$	0.604	0.833	0.947

the model first, followed by the factor representing temperature (Temp). The possible effect of using a number of tanks for the experiments was tested by including tanks in the analysis as a blocking factor uniquely identified for (or nested within) each temperature treatment (Temp·Tank). The effect of initial weight (wt) or log initial weight (ln(wt)) was then tested given that the grand mean and temperature are already in the model. The fifth and sixth lines in this part of the table give the results of fitting initial weight or its logarithm without temperature in the model. The "First difference in deviance" column given in the tables refers to the amount of deviance accounted for by the associated covariate or factor.

The column labelled "P level" refers to the χ^2 test used to assess the explanatory power of any one covariate or factor. The column labelled "Scale" gives the scale parameter, which relates the mean to the variance and is estimated here by the mean deviance. The scale parameter is defined to be equal to 1 for the binomial distribution, and the estimates given in Tables 2 and 3 indicate that there is some overdispersion present with respect to that expected for the binomial distribution. The models were initially fitted with the scale parameter equal to 1. Corrections for overdispersion as per Williams (1982) result in larger standard errors for the parameter estimates. Hence, factors or covariates found to be not significant when the scale parameter equals 1 will also be rejected when overdispersion

TABLE 6. Analysis of deviance for average amount of food eaten over feeding days only. Variables defined as follows: μ = grand mean; Temp = temperature; Temp·Tank = experimental tanks nested within temperature; ln(wt) = natural logarithm of initial weight.

(a) Gamma error with log link (scale = mean deviance)

Model	First difference in deviance	Degrees of freedom	*P* level	Scale
μ				5.68
+Temp	43.92	2	0.017	5.37
+Temp·Tank	408.60	21	0.000	1.85
+ln(wt)	72.65	1	0.000	0.99
+ln(wt)	493.50	1	0.000	1.08
+Temp	5.96	2	0.057	1.04
+Temp·Tank	25.74	21	0.210	0.99

(b) Parameter estimates for final model: $\beta_0 + \beta_1[\ln(wt)]$ (scale = 1.078)

Parameter	Estimate	Standard error
β_0	−1.660	0.212
i_1	0.655	0.032

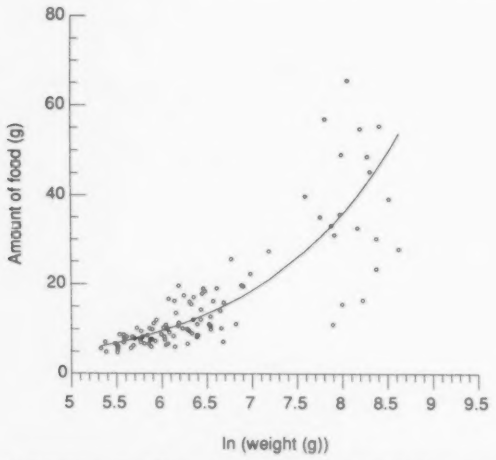

FIG. 4. Comparison of the predictions from the model of average meal size as a function of the natural logarithm of weight of the fish with the observed average amount of food eaten on feeding days.

is accounted for. The final model was adjusted for the overdispersion using the methods given in Williams (1982) in which the estimation method depends only on the relationship between the expectation and the variance. This approach avoids the need to specify a distribution which exhibits such a relationship. The final fit after adjustment was tested by a χ^2 test as per Williams (1982).

The analyses of deviance showed that in all cases the frequency of feeding is related to the temperature and not the size of the animals because neither initial weight nor its logarithm was important once temperature was accounted for. The effect of using the different tanks was neglible. The estimates for the scale parameter along with the parameter estimates are given for the final models in the bottom sections of Tables 2–4.

The predicted values for the probability of feeding from the final models are given in Table 5. In all three cases the

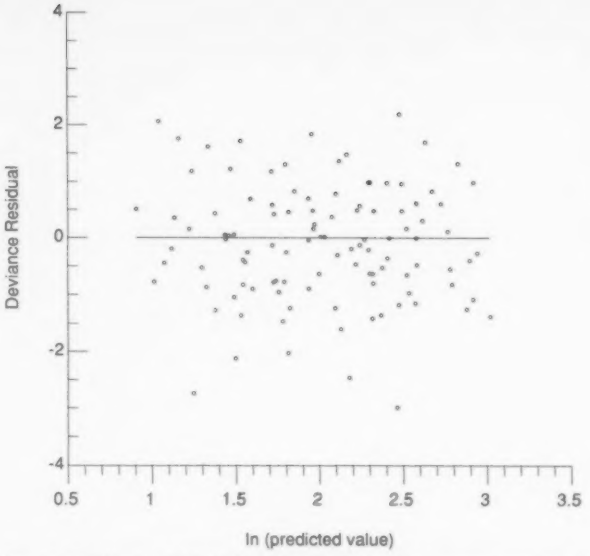

FIG. 5. Deviance residuals from the model for the average amount of food eaten on feeding days plotted against the natural logarithm of the predicted values of the model.

frequency is positively related to temperature. Note that for the unconditional $Pr[(feed)_t]$ and the conditional $Pr[(feed)_t|(feed)_{t-1}]$ the estimates of P_i are very similar at 4 and 8°C. At 1°C the P_i for the latter measure of feeding frequency is lower than that for the former, indicating that at 1°C the feeding behaviour on day t may not have been independent of what happened on the day before. The estimated frequencies for $P[(feed)_t|(not\ feed)_{t-1}]$ are all higher than for the above two measures. This appears to be consistent with higher digestion rates at the higher temperatures. That is, given that a fish has missed one day of feeding, it will be more likely to feed on the next day than if it had not missed the feeding, and this probability is greater for the higher temperatures.

Plots of deviance residuals against the adjusted fitted value, $2\sin^{-1}(\sqrt{\hat{P}_i})$ (McCullagh and Nelder 1983, p. 30 and 216), for the above three models were examined. There did not appear to be any indication of lack of fit or problems with the variance assumptions in these plots.

The results for the analysis of deviance of the average amount of food eaten for the model given in equation (2) are presented in Table 6. In contrast with the cases for frequency of feeding, temperature is not important once ln(initial weight) has been entered into the model. The grouping of fish by size into the different tanks resulted in some aliasing of tank effects and size (i.e. ln(wt)) effects. This was why Temp·Tank was significant when entered into the model before ln(wt) but not significant when ln(wt) was already in the model. We concluded that once size was taken into account, there were no effects due to the use of the tanks.

The observed and fitted points are plotted against ln(initial weight) in Fig. 4. Note that the scatter increases with the mean amount eaten, as expected assuming that the observations follow a gamma distribution. The deviance residuals are plotted against $\ln(\hat{y})$, (McCullagh and Nelder 1983) in Fig. 5. There are three residuals which are less than −2 in Fig. 5, the largest of which is obvious in Fig. 4 as the point at coordinate (7.9, 11). A number of fish either lost a small amount of weight or

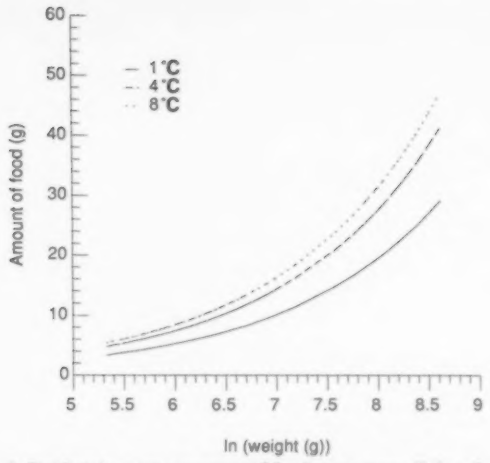

FIG. 6. Predicted average amount of food eaten over all days by each fish as a function of the natural logarithm of fish weight from the model in equation (3) for each of the temperatures in the experiment. Probability of feeding taken from the unconditional estimates in Table 5.

remained the same weight with respect to their preacclimation weight, over the experiment. Weight lost was always associated with negative residuals. The three extreme negative residuals were for the three fish which lost the most weight. Fitting the model with and without these points changed the parameter estimates and their standard errors by negligible amounts. The estimate of the scale parameter was close to 1.0 which indicates that the distribution of the amount of food eaten on feeding days followed an exponential distribution, a special case of the gamma distribution.

The finding that temperature was not related to the average amount of food eaten appears to contradict the observation that maximum meal size increases with temperature for fish >1000 g. However, the occurrence of such larger meals was balanced by an increased frequency of smaller meals so that the averge amount of food eaten remained unchanged.

The effect of once a day and twice a day feeding (at 8°C) on the average amount eaten on feeding days was tested in a similar way to the above. There was no significant difference between the average amount eaten per day for the two feeding regimes.

The final form of the model for estimating the average amount of food eaten by any fish ($\hat{y}_i$) of specified initial ln weight (x_i) and for any one of the j temperatures studied here is

$$(3)\quad \hat{y}_i = \hat{P}_j \times \exp(-1.660 + 0.6547x_i)$$

where $\hat{P}_j$ represents the probability of feeding for temperature j. The results of the analysis of feeding indicate that this probability is a function of the jth temperature only and not of any individual characteristic of the ith fish. What probability should be chosen from Table 5 for the $\hat{P}_j$ in equation (3) would depend on the purpose for which the prediction is being used. As noted above, there appeared to be little difference between $\Pr[(\text{feed})_t]$ and $\Pr[(\text{feed})_t|(\text{feed})_{t-1}]$ for temperatures of 4 and 8°C. However, the differences do appear to be larger for 1°C. Predicted values from the model in equation (3) for the range of weights used in this experiment are given in Fig. 6 for the three temperatures and the unconditional probabilities in Table 5. The general pattern would remain the same for the other probabilities.

Discussion

The decrease in food consumption associated with decreased temperature has been shown for a number of fish species including cod (Brown et al. 1989; Jobling 1988; Kohler 1965; Soofiani and Hawkins 1982), jack mackerel (*Trachurus symmetricus*) (Ishiwata 1984), and rainbow trout (*Oncorhynchus mykiss*, previously *Salmo gairdneri*) (Grove et al. 1978). That decreased consumption by cod, associated with decreased temperature, was primarily a function of decreased meal frequency rather than decreased average meal size contrasts with the findings of Mackenzie (1938) who showed that cod ate smaller meals at low temperatures. However, this apparent contradiction can be explained by accounting for the effect of temperature on food particle size preference. Mackenzie showed that at about 1°C, cod were often unable to swallow large herring pieces which were normally eaten at higher acclimation temperatures. The decrease in meal size due to problems of ingesting large pieces was presumably not a problem in this experiment, where the average weight of each shrimp was less than 4.5 g. However, the observation of decreasing food consumption associated with decreasing temperature is consistent with results for dab (*Limanda limanda*) (Gwyther and Grove 1981) and brown trout (*Salmo trutta*) (Elliott 1975). This suggests that at least in juvenile cod, control of food intake at low temperatures is governed by the degree of stomach fullness which in turn is related to the digestion rate. Grove et al. (1978) found that for rainbow trout the stomach emptying curve was a mirror image of the return to appetite curve. Warmer temperatures resulted in the faster return of appetite. A positive correlation between temperature and gastric evacuation rate has been established for several species including cod (Tyler 1970), dab (Gwyther and Grove 1981; Jobling et al. 1977), turbot (Fletcher et al. 1984; Grove et al. 1985), and perch (*Perca fluviatilis*) (Persson 1981).

Wide variation in meal size, i.e. where no feeding or a small feeding followed a large feeding, indicates that the stomach has not yet been depleted sufficiently to receive a large meal (Braaten and Gokstad 1980). The significant difference at 1°C between the probability of feeding ($P[(\text{feed})_t]$ and $P[(\text{feed})_t|(\text{feed})_{t-1}]$ suggests that, in contrast with the situation at 4 and 8°C, food in the stomach from the day before had not been depleted enough after 24 h to cause a return of appetite. This could explain why the maximum meal size was lower at 1°C for the larger fish. Presumably at some point between 1 and 4°C the required period for depletion is less than 24 h and the conditional and unconditional probabilities of feeding become equivalent.

It is difficult to compare published values for satiation level due to difference in food type, body size, temperature ranges, and feeding regimes. A reanalysis of data from Kohler (1965) reveals estimates of maximum ration of 1.23, 0.80, and 0.64% of body wt·d^{-1} at 12, 8, and 4°C, respectively. Kohler's study used cod with initial body weights of 1146–1200 g and frozen herring as food. The cod were fed only three times a week. The comparable values from our study for 8 and 4°C are higher (1.48 and 1.28% of body wt·d^{-1}, respectively). The predictions from equation (3) for food consumption values are comparable with those generated by Jobling's (1988) multiple regression model. Jobling's model predicts daily food con-

TABLE 7. Comparison of predictions of food intake ($kJ \cdot d^{-1}$) from the model of Jobling (1988) and equation (3) of this paper. Parenthetical values at 1°C indicate predictions beyond the range of temperatures studied by Jobling (1988).

Weight (g)	Model	Temperature 1°C	4°C	8°C
250	Equation (3)	19.97	28.25	32.15
	Jobling (1988)	(20.74)	28.14	40.57
500	Equation (3)	31.45	44.47	50.61
	Jobling (1988)	(36.16)	49.06	70.72

sumption in units of kilojoules per day and therefore, predictions from equation (3) have been converted to the same units by using the equation $k = wpc_1c_2$. In this equation, w is the average weight (wet) of *Pandalus* eaten on any one day as predicted by equation (3), P is the conversion factor from wet to dry weight ($p = 0.27$; K. G. Waiwood, unpubl. data), c_1 is the caloric content of 1 g of dry shrimp ($c_1 = 4610$ cal·g^{-1}; Tyler 1973), and c_2 is the conversion factor from calories to joules (4.184 J·cal^{-1}). Predictions for two sizes of fish (250 and 500 g) from both models are presented in Table 7. The predictions from both models agree closely at 4°C and are reasonably close for 1°C despite the fact that Jobling (1988) did not have data for this temperature. The greater discrepancy at 8°C may be due to differences in the time of year that our experiment and those used by Jobling were carried out. Waiwood (1978) showed that cod acclimated to constant temperatures exhibited decreased appetite in winter and spring.

One of the main advantages of the model in equation (3) is the decoupling of temperature characterized as frequency of feeding from the effect of the size of the cod. This simplifies studying the consequences of different temperature regimes on ration size when using bioenenergetic models. In contrast with our approach, Jobling's (1988) model includes temperature as terms in a polynomial of the form $0.104(\text{Temp}) - 0.000112(\text{Temp})^3$. We believe that expressing temperature effects as a cubic term is not as easily interpreted or as parsimonious as the frequency of feeding characterization used in equation (3). This characterization also offers a natural limit to feeding as a consequence of increased temperature. That is, the fish can only eat to a maximum of the number of times that they are fed. Treating temperature as covariate as per Jobling (1988) has no such limit on it.

Our finding that feeding twice a day did not result in a significant increase in food consumption indicates that at least for 8°C, maximum feeding levels can be estimated from a once a day feeding regime. This finding was supported by Braaten and Gokstad (1980), who found for periods up to 24 h that cod regulated their daily intake regardless of the time intervals between feeding.

Cod culture in Canada has been centered at Bay Bulls and the Northern Peninsula, Newfoundland (Waiwood et al. 1988). The harvest in 1988 was about 394 metric tons (Yeatman 1989). One- to 2-kg fish are caught in the local inshore trap fishery during May–August and held in sea pens where they double in weight over a 4-mo holding period. The fish are usually slaughtered before the water temperature falls below 4°C. One factor that must be considered, if the holding period is to be increased, is whether feeding and growth will continue at the lower temperatures. Our model suggests that at 4°C, nonmaturing fish will continue to feed at levels similar to 8°C and show only an approximate 30% reduction in feeding at 1°C. Our results further indicate that feeding once daily may result in high day to day variability in consumption and suggest that feeding frequency should be reduced at lower temperatures to avoid feed wastage.

The model presented here represents a starting point for estimating feeding levels for temperatures in the range 1–8°C. Further refinements would improve the model's utility including the use of actual culture conditions, feed types, and operating temperatures.

Acknowledgements

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Marine Distribution of the Sea Lamprey (*Petromyzon marinus*) in the Northwest Atlantic

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Halliday, R. G. 1991. Marine distribution of the sea lamprey (*Petromyzon marinus*) in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 48: 832–842.

Catch data from trawling surveys by the Canadian Department of Fisheries and Oceans and the U.S. National Marine Fisheries Service conducted between Nova Scotia and Cape Hatteras mainly during 1978–90 contained 60 records of sea lamprey (*Petromyzon marinus*) captures. A further 20 records were obtained from a variety of other sources. These animals ranged in length from 12 to 84 cm. Those less than 39 cm were almost all taken in bottom trawl surveys on the continential shelf or in coastal trap nets whereas most animals 56 cm and larger were caught in midwater trawls primarily along the shelf edge and over the continental slope. The data are consistent with a previously proposed 2.5-yr marine juvenile parasitic period but a 1.5-yr period cannot be ruled out until intermediate-sized animals 39–55 cm are caught. Direct and indirect evidence on host species indicates that feeding on anadromous and small marine fish may be restricted to the first juvenile year and that large pelagic fish and marine mammals are hosts at older ages. Thus, subsequent to the first winter following metamorphosis, sea lampreys are apparently pelagic in habit and possibly wide ranging in distribution in association with large pelagic hosts.

Parmi les données recueillies lors de relevés au chalut effectués essentiellement de 1978 à 1990 par le ministère des Pêches et Océans du Canada et le service des pêches marines nationales des États-Unis entre la Nouvelle-Écosse et Cape Hatteras, on a noté 60 captures de grandes lamproies marines (*Petromyzon marinus*). À ces prises s'ajoutent 20 autres captures signalées dans diverses autres sources. La longueur de ces lamproies allait de 12 à 84 cm. Celles de moins de 39 cm de longueur ont presque toutes été capturées lors de relevés au chalut de fond, dans la zone de la plate-forme continentale, ou au filet-trappe, dans la zone côtière, tandis que la plupart de celles qui mesuraient 56 cm ou plus ont été capturées au chalut flottant, principalement en bordure de la plate-forme et dans la zone du talus continental. Les données recueillies concordent avec l'hypothèse selon laquelle le stade juvénile de parasitisme marin durerait 2,5 ans, mais on nepeut éliminer la possibilité d'un stade de 1,5 ans à moins de capturer des spécimens de taille intermédiaire, soit de 39 à 55 cm. D'après les données directes et indirectes qu'on possède sur les espèces hôtes, les lamproies ne se nourriraient aux dépens d'espèces anadromes et de petits poissons marins que durant la première année du stade juvénile, les grands poissons pélagiques et les mammifères marins leur servant d'hôtes à un âge plus avancé. Ainsi, après le premier hiver suivant la métamorphose, la grande lamproie marine deviendrait pélagique et son aire de distribution, comme celle des grandes espèces pélagiques hôtes, serait étendue.

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The distribution of anadromous sea lampreys (*Petromyzon marinus*) during their marine phase is poorly known. On the basis of 22 documented records from the Atlantic seaboard of North America and anecdotal information, F. W. H. Beamish (1980) stated that marine observations of sea lampreys are mainly from shallow coastal waters and that these are predominantly of small specimens less than 40 cm in length. However, small sea lampreys in the size range 20–40 cm were also taken in bottom trawl catches on offshore banks in depths of 200 m or less whereas larger specimens (58–65 cm) were recorded in bottom trawl catches from deeper water (247–645 m).

There are several records of sea lampreys being caught in nets fished off the sea bottom. The first of these appears to be that of Murray and Hjort (1912) who recorded one taken "in the surface waters off the banks of Newfoundland" in 1910. The capture of a single specimen in an Isaacs–Kidd trawl fished at 330 m over a bottom depth of 2500 m off Ireland in the northeast Atlantic (Lelek 1973) established pelagic occurrence off the continental shelf. Haedrich (1977) reported a bottom trawl caught specimen at 4099 m, 400 km off southern New England, but acknowledged the possibility that capture occurred in midwater upon net retrieval. Two of F. W. H. Beamish's (1980) records are of sea lampreys taken off-bottom in Isaacs–Kidd nets and he speculated that sea lampreys taken in bottom trawls could have entered the net in midwater during the setting and hauling process. Despite these speculations, however, the current perception is that sea lampreys typically have a coastal, benthic distribution during their juvenile marine period.

A series of midwater trawl surveys of the mesopelagic fauna in deep water off the Scotian Shelf (Fig. 1), conducted during 1984–89 by the Canadian Department of Fisheries and Oceans (DFO), caught several sea lampreys. This confirmed that Lelek's (1973) record was not a stray occurrence but that lampreys regularly occur pelagically off the continental shelf over depths of 1000 m or greater. These captures prompted a search

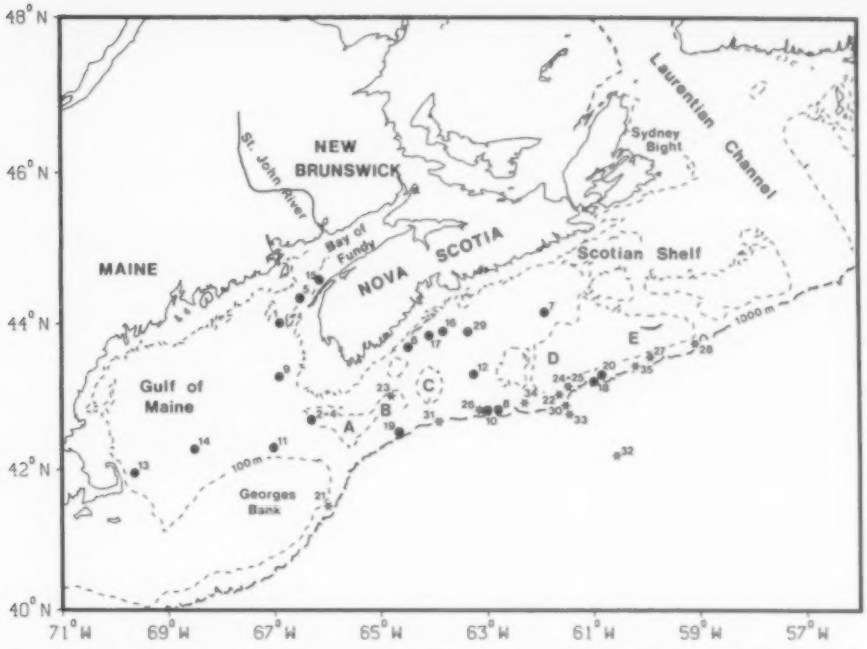

FIG. 1. Distribution of sea lamprey captures in DFO trawl surveys and some locations mentioned in text. Circles are bottom trawl catches, asterisks are midwater trawl catches, and numbers are reference numbers from Table 1. A = Browns Bank, B = Baccaro Bank, C = LaHave Bank, D = Western Bank, E = Sable Island Bank.

of catch data from a number of DFO and U.S. National Marine Fisheries Service (NMFS) surveys conducted between Nova Scotia and Cape Hatteras by both bottom and midwater trawls for sea lamprey catch records. A search for catch records from other sources such as the commercial fishery was also conducted. The resultant catch observations, which update F. W. H. Beamish's (1980) list of marine captures, provide new insights on marine distribution and a basis for suggestions concerning growth rate and feeding strategies during this life history period.

Methods

Bottom Trawl Surveys

In the study area the outer edge of the continental shelf is marked by an abrupt change in gradient at a depth of about 200 m. Seaward, the continental slope descends steeply to about 2000 m where it merges with the continental rise. Both DFO and NMFS standardized seasonal bottom trawl surveys cover all shelf and upper slope areas to a depth of 366 m (Azarovitz 1981; Halliday and Koeller 1981). Surveys by DFO extend from Sydney Bight to Georges Bank (Fig. 1) whereas NMFS surveys extend from southwest Nova Scotia to Cape Hatteras (Fig. 2). The innermost coastal shelf area shallower than about 90 m off the Canadian coast is excluded from these surveys, as it is generally too rough for bottom trawling. Off much of the U.S. coast, surveys extend close to shore into depths as shallow as 10 m, although north of Cape Cod the coastal zone to depths of 30 m or deeper is inaccessible to trawling. Catch data from three series of DFO surveys conducted in spring (predominantly March), summer (predominantly July), and autumn (predominantly October) and two series of NMFS surveys conducted in spring (predominantly March–April) and autumn (September–mid November) were examined for occurrence of sea lampreys. In addition, catch data from a series of deeper bottom trawl surveys conducted by DFO on the upper continental slope between the Laurentian Channel and Browns Bank (Fig. 1) were examined. The upper depth range of these surveys overlapped with the shelf surveys but over 50% of the trawl tows were in the range 366–1100 m. Most sampling was in October–November (580 tows) but some was in February–March (100 tows) and a small amount in August–September (30 tows). Data from a series of bottom trawl surveys for Atlantic herring (*Clupea harengus harengus*) conducted by NMFS primarily in shallow coastal waters between Maine and Delaware Bay in winter (mid-January–February) and a gear comparison cruise conducted by NMFS in December 1986 were also examined. An Atlantic Western IIa trawl was used for DFO surveys except for summer surveys prior to 1982 which were conducted with a Yankee No. 36 trawl. During the period for which NMFS data were examined (1982–90), surveys were conducted using a Yankee No. 36 trawl. These nets have a wingspread of about 11 m and a headline height of 4.5–5.0 m in the case of the Western IIa and of 2.5–3.0 m in the case of the Yankee No. 36 (Azarovitz 1981; Carrothers 1988).

Midwater Trawl Surveys

Catch data from three midwater trawl survey series conducted by DFO were examined for records of sea lampreys. One of these, directed towards juvenile Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), covered

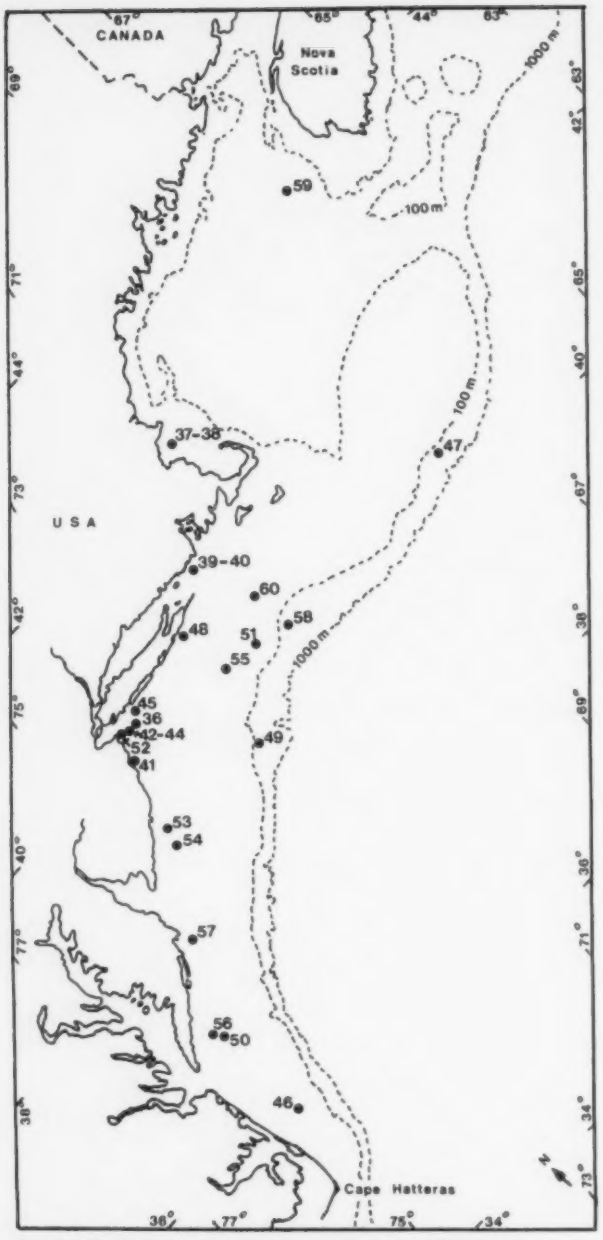

FIG. 2. Distribution of sea lamprey captures in NMFS trawl surveys. Numbers are reference numbers from Table 1.

variable areas off southwestern Nova Scotia from LaHave Bank to the mouth of the Bay of Fundy and south to Georges Bank (Fig. 1) mainly in June but with some sampling in July and August. A second series, directed towards juvenile silver hake (*Merluccius bilinearis*), concentrated sampling in the central shelf area from Western Bank to LaHave Bank but some surveys covered all of the Scotian Shelf. Most of these silver hake surveys were conducted by USSR vessels under cooperative arrangements. Sampling was almost exclusively in October–November but one Canadian and one USSR cruise were conducted in January. The third midwater survey series was that directed towards the mesopelagic fauna off the Scotian Shelf. Most sampling was conducted in an area between 59 and 63°W and 40°N to the shelf edge (Fig. 1) but sampling did extend as far east as the Grand Bank. Some samples were collected in February, April, and June (55, 14, and 27 tows, respectively) but 70% were spread fairly evenly over July–December. The predominant gear used in all of these midwater surveys was the International Young Gadoid Pelagic Trawl (IYGPT), a research midwater trawl with a typical vertical mouth opening of 10 m and wingspread of 12 m. However, the USSR surveys during 1978–80 were conducted using a Soviet 13.6-m juvenile ("fry") trawl with vertical and horizontal mouth openings of 6 and 8 m, respectively (Noskov and Sherstyukov 1984). The typical IYGPT tow in the shelf survey series was stepped-oblique (with three steps) from near-bottom to surface but silver hake surveys used near-bottom tows only until 1981. Details of survey methods for the two shelf survey series are given by Koeller et al. (1986). The standard off-shelf survey tow was also a three-step oblique with steps at 200, 100, and 50 m but horizontal tows were also made at depths as great as 1000 m.

Oceanographic Data

Water temperature and salinity data cited were collected using a variety of mechanical and expendable bathythermographs, reversing water bottles, and conductivity–temperature–depth recorders routinely used on bottom and midwater trawl surveys.

Other Catch Data Sources

The DFO International Observer Programme (IOP) places fisheries observers aboard mainly foreign commercial vessels to observe, among other things, the composition of catches. Records from this programme for the area off Nova Scotia during 1977–89 were searched for sea lamprey occurrences. Searches were also conducted of records at the Nova Scotia Museum, Halifax, N.S., of the personal records of W. B. Scott, Huntsman Marine Science Centre, St. Andrews, N.B., and of the photograph collection at the DFO Biological Station, St. Andrews, N.B.

Results

A total of 80 captures of sea lampreys were recorded in the data series examined (Tables 1 and 2), 46 in bottom trawl surveys, 14 in midwater trawl surveys, and 20 in other data sets.

Bottom Trawl Survey Catches

Of the 21 sea lampreys caught in DFO bottom trawl surveys, 12 occurred in spring surveys on the Scotian Shelf and two in spring surveys on Georges Bank. Summer bottom trawl surveys took only three specimens, despite the larger number of tows made, and autumn surveys took none. These surveys employed identical methodologies, and therefore, catch rates (13.7, 1.0, and 0.0 animals per 100 tows in March, July, and October, respectively) can be taken as a measure of the seasonal availability of sea lampreys to bottom trawl gear fished on the shelf to depths of 366 m. Slope bottom trawl surveys caught three specimens, two of which resulted from the small amount of sampling in August–September. A further bottom trawl caught specimen was taken during a silver hake survey in January 1981. These bottom trawl caught specimens were taken over a

TABLE 1. Occurrences of sea lampreys in DFO and NMFS trawl surveys. BT = botton
Pelagic Trawl, Y36 = Yankee No. 36 trawl. A (1) in the fish length column indica

Survey series (years)	No. of tows in series	Specimen Reference No.	Date	Time (local)	Gear	°/
DFO surveys						
Spring BT, Scotian Shelf (1979–85)	870	1	7 Mar. 1979	11:25	WIIa	44
		2	10 Mar. 1979	11:35	WIIa	42
		3	10 Mar. 1979	11:35	WIIa	42
		4	10 Mar. 1979	11:35	WIIa	42
		5	27 Mar. 1980	06:05	WIIa	44
		6	13 Mar. 1981	06:45	WIIa	43
		7	3 Mar. 1982	21:15	WIIa	44
		8	9 Mar. 1982	18:25	WIIa	42
		9	10 Apr. 1983	11:25	WIIa	43
		10	5 Mar. 1984	19:15	WIIa	42
		11	23 Mar. 1984	18:05	WIIa	42
		12	6 Mar. 1985	19:55	WIIa	43
Spring BT, Georges Bank (1986–89)	430	13	10 Mar. 1986	03:45	WIIa	41
		14	9 Mar. 1988	05:35	WIIa	42
Summer BT, Scotian Shelf (1970–88)	2900	15	11 July 1981	13:05	Y36	44
		16	5 July 1988	02:55	WIIa	43
		17	5 July 1988	04:45	WIIa	43
Autumn BT, Scotian Shelf (1979–84)	790	No captures				
BT, slope (1982–89)	710	18	26 Nov. 1982	01:55	WIIa	43
		19	24 Sept. 1985	07:20	WIIa	42
		20	23 Sept. 1987	15:34	WIIa	43
MWT, juvenile gadids (1983–88)	440	21	8 June 1984	—	IYGPT	41
Canada–USSR, autumn juvenile silver hake MWT (1978–89)	1625	22	4 Oct. 1978	12:50	Fry trawl	43
		23	17 Oct. 1980	14:50	Fry trawl	43
		24	6 Nov. 1982	21:05	IYGPT	43
		25	6 Nov. 1982	21:05	IYGPT	43
		26	10 Nov. 1983	05:15	IYGPT	42
		27	5 Nov. 1984	22:37	IYGPT	43
		28	9 Nov. 1989	18:55	IYGPT	43
Canada, January juvenile silver hake (1981)	28 MWT 12 BT	29	12 Jan. 1981	21:00	WIIa	43

= bottom trawl, MWT = midwater trawl, WIIa = Western IIa trawl, IYGPT = International Young Gadoid
n indicates one specimen caught but not measured; weights were measured at sea and are not precise.

	Position		Bottom depth (m)	Bottom temperature (°C)	Bottom salinity (‰)	Sea lamprey data		Remarks
	°'N	°'W				Length (cm)	Weight (gm)	
	44 01	66 53	135–146	3.9	32.4	(1)	—	
	42 41	66 18	77–88	2.8	33.5	26	—	
	42 41	66 18	77–88	2.8	33.5	27	—	
	42 41	66 18	77–88	2.8	33.5	30	—	
	44 20	66 30	205	4.4	33.1	29	—	
	43 41	64 28	130–152	4.6	33.1	17	—	
	44 09	61 55	143–150	8.4	34.6	25	—	
	42 50	62 49	188–198	9.3	34.9	27	—	
	43 16	66 53	168–190	6.9	33.9	27	—	
	42 48	63 01	256–294	6.5	35.0	27	—	
	42 19	67 00	295–315	7.7	—	33	—	
	43 19	63 14	155–170	9.8	35.1	32	—	
	41 57	69 38	199–205	5.8	33.5	(1)	—	
	42 17	68 30	176	6.7	33.9	(1)	—	
	44 35	66 06	80–86	8.3	32.5	35	—	
	43 54	63 49	172–183	8.2	34.5	31	—	
	43 51	64 04	152–163	6.6	34.0	26	—	
	43 13	60 58	457–503	—	—	(1)	—	Net off bottom
	42 30	64 38	227–274	—	—	70	600	
	43 18	60 50	243–252	—	—	64	—	
PT	41 29	65 59	135–154	—	—	61	—	Net depth 124–0 m
rawl	43 02	61 37	298	8.9	—	68	—	
rawl	43 01	64 47	81–90	8.2	—	73	—	
PT	43 08	61 28	210–220	6.3	—	69	—	} Combined weight = 1.3 kg
PT	43 08	61 28	210–220	6.3	—	77	—	
PT	42 49	63 06	207–217	9.8	—	72	700	
PT	43 33	59 55	235–295	8.5	—	62	400	
PT	43 44	59 04	200–205	—	—	78	700	
	43 54	63 20	139–141	8.5	34.4	20	—	

TABLE 1. (*Concluded*)

Survey series (years)	No. of tows in series	Specimen Reference No.	Date	Time (local)	Gear	Positi °'N
Off-shelf, MWT (1984–89)	307	30[a]	23 Oct. 1988	19:57	IYGPT	42 53
		31[a]	26 Oct. 1988	04:38	IYGPT	42 39
		—	Nov.–Dec. 1988	—	IYGPT	—
		32[a]	8 June 1989	22:10	IYGPT	42 11
		33[a]	9 June 1989	07:21	IYGPT	42 46
USSR, January juvenile silver hake (1990)	50 MWT	34	5 Jan. 1990	04:25	IYGPT	42 57
		35	7 Jan. 1990	18:15	IYGPT	43 26
NMFS surveys						
Winter BT, coastal herring (1982–84)	806	36	22 Jan. 1982	21:51	Y36	40 24
		37	5 Feb. 1982	09:30	Y36	42 20
		38	5 Feb. 1982	09:30	Y36	42 20
		39	15 Feb. 1983	12:32	Y36	41 16
		40	15 Feb. 1983	12:32	Y36	41 16
		41	21 Feb. 1984	20:36	Y36	40 01
Spring BT, Maine to Hatteras (1982–90)	3303	42	30 Mar. 1983	11:30	Y36	40 26
		43	30 Mar. 1983	11:30	Y36	40 26
		44	30 Mar. 1983	11:30	Y36	40 26
		45	30 Mar. 1983	12:37	Y36	40 30
		46	3 Mar. 1984	10:20	Y36	36 02
		47	25 Mar. 1985	02:24	Y36	40 21
		48	7 Apr. 1987	02:22	Y36	40 51
		49	9 Apr. 1987	05:49	Y36	39 24
		50	5 Mar. 1988	17:14	Y36	37 10
		51	23 Mar. 1988	08:11	Y36	40 06
		52	7 Mar. 1989	11:14	Y36	40 23
		53	12 Mar. 1989	12:17	Y36	39 23
		54	12 Mar. 1989	16:17	Y36	39 07
		55	14 Mar. 1989	09:17	Y36	40 06
		56	14 Mar. 1989	20:25	Y36	37 14
		57	15 Mar. 1990	13:11	Y36	38 12
		58	19 Mar. 1990	12:59	Y36	40 03
		59	15 Apr. 1990	07:43	Y36	43 34
Autumn BT, Maine to Hatteras (1982–89)	3169	No captures				
Gear comparisons (1986)	—	60	7 Dec. 1986	12:30	Y36	40 30

[a]Specimens deposited in Nova Scotia Museum, Cat. No. 10083-85.
[b]Temperature range in top 200 m.

Position		Bottom depth (m)	Bottom temperature (°C)	Bottom salinity (‰)	Sea lamprey data		Remarks
°'N	°'W				Length (cm)	Weight (gm)	
42 53	61 30	1200	10.8–14.0[b]	—	84	750	Net depth 206–0 m
42 39	63 54	1000	2.8–10.9[b]	—	72	650	Net depth 210–0 m
—	—	—	—	—	—	—	At least 1 specimen taken; records lost
42 11	60 33	4000	11.1–14.9[b]	—	56	200	Net depth 200–0 m
42 46	61 26	1900	11.9–14.6[b]	—	65	350	Net depth approx. 1000 m
42 57	62 20	135	9.1	—	25	—	
43 26	60 13	250	9.1	—	80	1000	
40 24	73 40	25	—	—	17	—	
42 20	70 47	37	2.4	—	19	—	}Combined weight = 200 g
42 20	70 47	37	2.4	—	20	—	
41 16	71 41	37	—	—	16	—	}Combined weight = 100 g
41 16	71 41	37	—	—	17	—	
40 01	74 01	—	—	—	75	1000	
40 26	73 42	26	5.2	—	17	—	
40 26	73 42	26	5.2	—	20	—	
40 26	73 42	26	5.2	—	24	—	
40 30	73 38	17	5.3	—	14	—	
36 02	75 03	41	14.9	—	13	—	
40 21	68 00	145	—	—	22	100	
40 51	72 23	19	—	—	16	—	
39 24	72 30	130	11.4	—	20	100	
37 10	75 26	28	—	—	17	—	
40 06	71 43	86	10.3	—	24	100	
40 23	73 56	15	3.6	—	20	—	
39 23	74 13	21	—	—	19	—	
39 07	74 14	25	4.4	—	18	—	
40 06	72 10	73	—	—	70	700	
37 14	75 35	18	—	—	21	—	
38 12	74 56	22	—	—	18	—	
40 03	71 05	234	11.8	—	19	—	
43 34	66 59	182	6.7	—	38	300	
40 30	71 16	71	—	—	16	—	

wide depth range. However, the deepest trawl tow in which a sea lamprey was taken (Table 1, Ref. No. 18: 457–503 m) caught in addition only mesopelagic fish, and thus it is unlikely that the trawl was fishing on bottom. If this record is discounted, the depth range of captures was 77–315 m, with almost 60% of specimens (12) taken between 130 and 205 m. Captures were widespread in the Gulf of Maine from the mouth of the Bay of Fundy to north of Georges Bank, in the central Scotian Shelf, and along the shelf edge (Fig. 1). Bottom temperatures at the locations of capture ranged from 2.8 to 9.3°C, with a median of 6.6°C. Salinities ranged from 32.4 to 35.1‰.

Of the 25 sea lamprey captures in NMFS bottom trawl surveys, six were caught in winter coastal herring surveys, 18 in spring, and none in autumn standardized shelf surveys and one specimen was caught during the December gear comparisons (Table 1). As in the case of DFO surveys, catch rates in the NMFS spring and autumn surveys are directly comparable with each other and the failure to capture sea lampreys in NMFS autumn surveys confirms their seasonal unavailability to bottom trawls in U.S., as in Canadian, waters. Most NMFS specimens (18) were taken coastally at depths of 41 m or less. Most of the coastal zone at these depths is outside the sampling area of DFO surveys. Specimens taken offshore were caught in 71–234 m, comparable with the depths of DFO captures. Sea lampreys were taken throughout the geographic range of the surveys from off southwestern Nova Scotia to 36°N (Fig. 2). Bottom temperatures at the locations of capture ranged from 2.4 to 14.9°C.

Midwater Trawl Survey Catches

The midwater trawl surveys conducted in shelf waters yielded 10 sea lampreys, nine from the silver hake juvenile surveys on the Scotian Shelf and one from juvenile cod and haddock surveys in the southwestern Nova Scotia – Georges Bank area. All but one of these captures were made along the shelf edge over depths of 135–295 m despite most survey coverage being on the shelf. The exception was a single specimen taken in 81–90 m on Baccaro Bank. As all sets included towing time near bottom, no inference can be made about where in the water column captures occurred. Midwater trawl surveys of the mesopelagic fauna south of the central Scotian Shelf in continental slope and deep ocean waters caught four specimens for which records are available. One or more additional specimens were taken on a cruise in November–December 1988 but the pertinent data were lost. Three of these sea lampreys were taken over bottom depths of 1000–4000 m in trawl tows made in the upper 200 m of the water column. The fourth specimen (Ref. No. 33) was caught in a tow during which the net fished at approximately 1000 m over a bottom depth of 1900 m. Measurements of trawl mouth opening indicate that the IYGPT net is probably fishing quite effectively during setting and retrieval, so this specimen could have been taken at any depth above 1000 m. Thus, with the possible exception of this specimen, pelagic captures in the three survey series were made in the top 300 m of the water column. The specimens caught in the October 1988 mesopelagic survey (Ref. Nos. 32, 33) were taken 35 and 130 km seaward of the 200-m isobath. The most distant record was 320 km from the coast of Nova Scotia. Bottom temperatures at the silver hake juvenile survey stations at which sea lampreys were caught ranged between 6.3 and 9.8°C. Temperatures in the top 200 m at the stations of sea lamprey capture off-shelf ranged between 10.8 and 14.9°C in three cases (Ref. Nos. 30, 32, 33) and between 2.8 and 10.9°C in the fourth (Ref. No. 31).

Other Catches

Other marine records (Table 2) include 10 sea lampreys taken immediately adjacent to the Nova Scotia coast, primarily in fish traps. An additional seven specimens were recorded by the IOP from foreign small-mesh bottom trawl catches in the silver hake and redfish (*Sebastes* spp.) fisheries. Captures in the silver hake fishery coincided with the concentration of survey captures along the shelf edge but this is not necessarily meaningful, as the fishery itself is constricted to this geographical area by regulation. The two specimens taken by the Japanese redfish fishery establish occurrence in the Laurentian Channel. Three other records were obtained of specimens (attached to hosts) caught on pelagic longline gear, two from IOP observations on the Japanese tuna fishery off the shelf edge south of LaHave Bank and one during research sampling off Cape Hatteras in winter.

Host Attachment

Four of the sea lampreys taken in coastal traps were attached to pelagic hosts, Atlantic herring, Atlantic mackerel (*Scomber scombrus*), Atlantic salmon (*Salmo salar*), and a basking shark (*Cetorhinus maximus*). The two specimens taken in the Japanese pelagic longline fishery off the edge of the Scotian Shelf were attached to a captured swordfish (*Xiphias gladius*) in one case and in the other to a captured bluefin tuna (*Thunnus thynnus*). The specimen taken during research pelagic longlining off Cape Hatteras was also attached to a captured swordfish.

In most cases there are no records concerning whether or not lampreys were attached to hosts when either survey or commercial trawl catches were brought aboard. However, seven of the sea lampreys taken on cruises (Ref. Nos. 10, 20, 28, 30–33) were observed to be unattached to hosts at the time the catch was released on deck. It is possible that sea lampreys could become detached from hosts between the time of capture and of release of the catch aboard ship. However, the five sea lampreys taken by midwater trawl (Ref. Nos. 28, 30–33) were by far the largest specimens in the catches of the tows in which they were taken. The remainders of these catches were small mesopelagic species, or juveniles of shelf species, which were unlikely to be suitable as hosts for sea lampreys. At least for these latter sea lampreys it can safely be concluded that they were free-swimming at the time of capture.

Host Scarring

There are no cases of potential host species being examined systematically for frequency of scarring as a result of attack by sea lampreys. However, W. B. Scott (pers. comm.) recollects that sea lamprey scars were observed on 3–5% of swordfish during research sampling conducted in the 1960s, and the photograph collection of the DFO Biological Station, St. Andrews, contains a number of photographs of such scars. P. Brodie (Bedford Institute of Oceanography, Dartmouth, N.S., pers. comm.) stated that sea lamprey scars are common on whales, particularly sei whales, observed off Nova Scotia.

Size of Sea Lampreys Caught

The total lengths of sea lampreys, recorded for 65 of the specimens caught, ranged from 12 to 84 cm (Tables 1 and 2). Lengths fell into two modal groups (Fig. 3): one group of 48

TABLE 2. Other marine records of sea lampreys. NSM = Nova Scotia Museum, HMSC = Huntsman Marine Science Centre, STABS = St. Andrews Biological Station.

Data source	Capture date	Lamprey data		Location	Remarks
		No.	Length (cm)		
J. Gilhen (NSM)	29 June 1965	1	29	Off Hopson Island (Prospect area), Halifax Cty, N.S.	Attached to a basking shark (*Cetorhinus maximus*) above and anterior to anal fin
	14 June 1969	1[a]	12	Off Burnt Island (Prospect area), Halifax Cty, N.S.	Attached to an Atlantic salmon (*Salmo salar*) taken in a bowl trap
	16 June 1974	1[a]	16	Off Black Point, St. Margarets Bay, Halifax Cty, N.S.	Attached to an Atlantic mackerel (*Scomber scombrus*)
	15 June 1982	3[a]	16, 19, 22	Off Crouchers Island, St. Margarets Bay, Halifax Cty, N.S.	Taken in a mackerel trap
	15 Nov. 1989	3[a]	14, 16, 16	Off Red Bank, St. Margarets Bay, Halifax Cty, N.S.	Taken in a mackerel trap, not attached to a host
W. B. Scott (HMSC); P. W. G. McMullon (STABS)	19 Apr. 1978	1	—	Liverpool Harbour, Queens Cty, N.S.	Taken in a herring trap attached to an Atlantic herring (*Clupea harengus harengus*); lamprey slightly smaller than herring
	Jan.–Feb. 1966	1	25–30	Northeast of Cape Hatteras	Attached to a swordfish (*Xiphias gladius*) at base of first anal fin; taken by surface longline on a DFO research cruise ATC111
IOP	4 Nov. 1987	1	—	Approximately 42°40′N, 64°10′W	Attached to a 259-cm swordfish (*Xiphias gladius*) taken by surface longline in Japanese tuna fishery
	18 Nov. 1988	1	—	Approximately 42°40′N, 63°40′W	Attached to the back of a bluefin tuna (*Thunnus thynnus*) taken by surface longline in Japanese tuna fishery
	Oct. 1984	2	—	Laurentian Channel, 430–455 m bottom depth	Taken in bottom trawl in Japanese redfish fishery
	Apr.–July 1986–89	5	—	South of Sable Island Bank and Western Bank, 120–280 m bottom depth	Taken in bottom trawl in USSR and Cuban silver hake fishery

[a]Measured after preservation.

animals between 12 and 38 cm (referred to below as small animals), all but one of which were caught in bottom trawl surveys or coastal traps, and a second group of 17 animals between 56 and 84 cm (large animals), all but four of which were taken in midwater trawl surveys. In the group of small animals, four specimens 14–16 cm were taken in coastal Nova Scotia traps and in NMFS gear comparisons in November–December. However, most of this group of animals was taken in winter and spring bottom trawl surveys. Those in NMFS winter and spring surveys were in most cases smaller than those in DFO spring surveys (Fig. 3). However, those taken in shallow water (<42 m) in NMFS surveys had an average length of 18.0 cm (n = 17) whereas those taken in the same depth range as DFO specimens averaged 24.6 cm (n = 5), not greatly different from the DFO captures which averaged 27.3 cm (n = 11). Specimens taken in June in coastal traps averaged only 19.0 cm (n = 6) whereas these taken in July DFO bottom trawl surveys were 30.7 cm (n = 3). In the group of large animals, those taken in June averaged 60.7 cm (n = 3) whereas those caught during September–November were 71.7 cm (n = 11). Those taken during January–March had an average length of 75.0 cm (n = 3).

Discussion

The size compositions of sea lampreys caught by bottom and midwater trawls were distinctly different (Table 1). This could result from differences in either vulnerability or availability to the gears as a function of size. The research trawls used had elliptical mouth areas which ranged between 25 and 95 m^2, but all were equipped with small-mesh liners or codends and were towed at about 3.5 knots. All these trawls were capable of catching a wide variety of fish in the size range from 2–3 cm to 1 m or more, i.e. including the full size range of sea lampreys caught. Although there is undoubtedly some variation in vulnerability with length of sea lampreys among gears, the differences in size composition between midwater and bottom trawl catches were sufficiently large that these cannot be ascribed to differences in gear selection. Thus the differences result from differences in the lengths of sea lampreys available to midwater and bottom trawls, i.e. to differences in the size of sea lampreys which occurred in the paths of the two trawl types. Small sea lampreys 38 cm and less have a low availability to midwater trawls, large animals greater than 55 cm have a low availability to bottom trawls, and those between these sizes are seldom

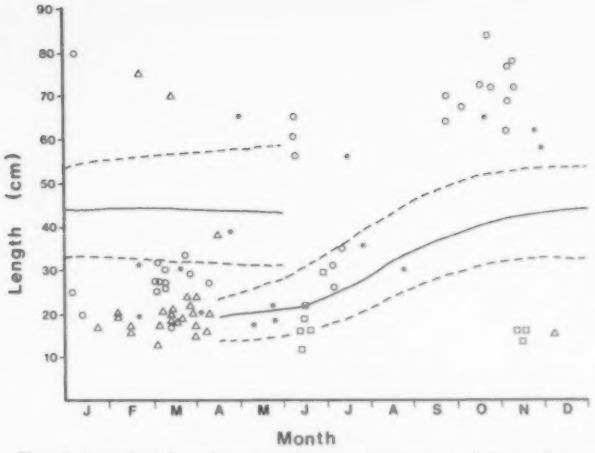

FIG. 3. Lengths of sea lampreys from marine waters of the northwest Atlantic by date of capture, compared with growth pattern in the Great Lakes. Circles = DFO records, triangles = NMFS records, squares = NSM records, asterisks = F. W. H. Beamish (1980) records. Great Lakes data from Applegate (1950): solid line is the mean, and the broken lines denote the range of observations.

caught by either gear type. As the survey series examined sampled intensively much of the continental shelf and upper slope over a variety of seasons and number of years, this observation regarding availability is clearly not an artifact resulting from poor sampling but, rather, reflects ontogenetic changes in distribution of the animals themselves.

Bottom catches of small sea lampreys indicate some size gradation between near-coastal and offshore shelf locations. This is particularly clear in NMFS winter and spring survey data where those specimens taken near the coast were over 6 cm smaller, on average, than those taken offshore. Also, specimens taken in Nova Scotian coastal traps in June were much smaller than those taken in adjacent offshore areas in July surveys. Thus, the sea lampreys taken in DFO spring surveys, which do not sample near-coastal areas, were likely in the upper size range of the marine population of small sea lampreys, i.e. 27.3 cm is an overestimate of the mean length of small animals in spring in Nova Scotia waters.

Sea lampreys have a broad temperature tolerance. F. W. H. Beamish (1980) cited a range of −0.6 to at least 20°C. The observation at the low end of this range was associated with a single bottom trawl caught specimen. The remainder of his marine specimens were caught at temperatures of 3.0–7.5°C. The minimum temperature record in present data is 2.4°C. There was an absence of sea lampreys in bottom trawl tows on the Scotian Shelf to the north and east of Sable Island Bank, despite extensive survey coverage (Scott 1988). This may be a reflection of the lower temperatures which occur there (Hachey 1942), deeper bottom temperatures remaining below 2°C even in summer (Scott 1976). Thus, 2.5°C may be a better approximation to the low end of the normal temperature range for sea lampreys in marine waters. The upper end of F. W. H. Beamish's (1980) temperature range was based on observations in freshwater. The present marine records give an upper observation of 14.9°C. Tolerance to temperatures up to 20°C raises the possibility of widespread distribution of sea lampreys in Slope Water, a body of warm water which lies between the continental slope off Nova Scotia and the Gulf Stream and which is characterized by water temperatures at 200 m between 9 and 15°C (Worthington 1964). Three specimens (Ref. Nos. 30, 32, 33) were captured in Slope Water. The locations of these captures suggest that sea lamprey distribution was restricted to a band adjacent to the shelf, but the intensity of sampling was too low to exclude the possibility of a more widespread distribution in Slope Water. The data do confirm that the pelagic occurrence of sea lampreys over the continental slope and deep ocean is a normal feature of their distribution and cast additional doubt that the sea lamprey reported by Haedrich (1977) was indeed captured on the bottom at a depth of 4099 m.

Interpretation of marine catch records in the context of sea lamprey life history requires a brief summary of the species' biology in freshwater. Metamorphosis of sea lampreys from the larval to the juvenile stage occurs between July and November when larvae reach lengths of 11–16 cm (Beamish and Potter 1975; Potter and Beamish 1977). This is followed by migration out of the river system although a portion may remain in the river in some cases. In the following spring and summer (May–September), juvenile anadromous sea lampreys typically in the size range 15–40 cm occur in rivers, primarily as parasites of migrating Atlantic salmon, alewives (*Alosa pseudoharengus*), and American shad (*Alosa sapidissima*) (F. W. H. Beamish 1980). F. W. H. Beamish (1980) concluded that this large variation in sea lamprey size reflects the different times of onset of feeding, rather than the presence of more than one year-class, the smallest animals being those which overwintered in rivers without feeding and the larger being those which had migrated to estuarine and marine waters in late autumn and commenced feeding. Anadromous sea lampreys larger than 40 cm occur in freshwater essentially only as nonfeeding adults during their spring spawning migration. Spawning occurs in a large number of rivers on the Canadian mainland from Quebec tributaries to the St. Lawrence River south to northern Florida on the Atlantic seaboard (F. W. H. Beamish 1980) and in at least one river which enters the Gulf of Mexico (Vladykov and Kott 1980). Spawning migrations occur between March and early July, with some reports from as late as September and with a trend toward later dates in more northern rivers. F. W. H. Beamish (1980) estimated that sea lampreys entering the St. John River, New Brunswick, in early April would have a mean length of about 83 cm and documented shrinkage during upstream migration, spent animals averaging 66 cm. Death follows spawning. Based on these observations and his marine records, F. W. H. Beamish (1980) proposed a growth pattern which requires a period of about 2.5 yr between metamorphosis and spawning. The landlocked form of the sea lamprey which occurs throughout the Great Lakes system has a parasitic period of about 1.5 yr (Applegate 1950). Applegate (1950) observed downstream migration of recently transformed specimens during October–April at a mean length of 14.5 cm (range 10–19 cm) and rapid growth from about 20 cm in June to 43 cm in November. There was no growth overwinter and upstream spawning migrants in April–June also averaged 43 cm in length.

The lengths of sea lampreys taken in marine waters (Tables 1 and 2, and from F. W. H. Beamish (1980)), plotted by date of capture, are compared with the growth pattern of landlocked sea lampreys given by Applegate (1950) in Fig. 3. F. W. H. Beamish's (1980) proposal for a 2.5-yr marine period in the anadromous form would be consistent with a growth pattern much the same as that of the landlocked form for the first 1.5 yr, followed by a further year of growth in the marine environment

during which length increased from about 45 to 80 cm. Some aspects of the data are consistent with such a growth pattern but there are apparent anomalies. The small animals, 14–16 cm, caught in November–December conform with the size expected of recent downstream migrants, and those taken in near-coastal areas during January–April NMFS surveys (mean length 18 cm) were largely within the size range of overwintering Great Lakes specimens. Those taken in deeper offshore waters in DFO and NMFS surveys during this same period were substantially larger, however, with a mean length of 26 cm. The observations by Potter and Beamish (1977) of animals of 13 cm mean length which overwintered in the St. John River and by Manseuti (1962) of animals 15–18 cm in estuarine conditions in Chesapeake Bay during winter months suggest that there is a gradation in size of postmetamorphic animals during their first winter, the largest specimens occurring furthest from natal rivers. Thus, those sea lampreys caught offshore during spring bottom trawl surveys may represent the upper extreme of the size range of first (postmetamorphic) year animals in that season. The 14 animals of length 35 cm or less taken during May–August conform fairly well to the Great Lakes growth curve. Most of these animals were taken in near-coastal waters; availability to the more offshore DFO bottom surveys was greatly reduced and even the three specimens which were caught in these surveys all occurred in tows from that part of the surveyed area closest to the coast (Fig. 1). Also in the May–September period, sea lampreys up to about 40 cm occur in a substantial number of rivers along the Atlantic seaboard (F. W. H. Beamish 1980). Mean length of specimens in the St. John River in June–July was about 27 cm (Potter and Beamish 1977), which also conforms to the Great Lakes curve. However, there were no captures of animals during September–March in the length range of the oldest Great Lakes animals. In April, two animals, caught in diverse locations, lay close to the size of Great Lakes spawning migrants, a 38-cm specimen taken by the NMFS bottom trawl survey at 183 m depth off southwestern Nova Scotia (Fig. 2) and the record by Haedrich (1977) of a 39.5-cm specimen taken off the continental shelf. (Breder's (1923) record is of a specimen 17 cm in length, not 43 cm as reported by F. W. H. Beamish (1980)). In the case of large animals, the four caught in June–July had a mean length of 60 cm, the 14 recorded from September–November averaged 70 cm, and the four taken during January–May averaged 73 cm. These last animals are close to the size recorded for spawning migrants in rivers (Potter and Beamish 1977).

Although these length data for sea lampreys caught in marine waters can be explained by F. W. H. Beamish's (1980) proposal for a 2.5-yr marine period, the lack of captures of medium-sized animals in what would be the second sea winter is an apparent anomaly. An alternative hypothesis is that marine growth is in fact completed in 1.5 yr. It could be argued that a greater array of suitable hosts permits faster growth in the marine environment than is possible for the derived landlocked form in freshwater. However, acceptance of this hypothesis requires that animals taken during June–August, which range in length from 12 to 65 cm, are to be considered as being of all the same (postmetamorphic) age. The animals 56–65 cm in length taken pelagically near the shelf edge in June are too small, taken too late in the year, and too far from rivers to be considered spawners in the year of capture. Although bottom survey data indicate that marine-caught animals have a broader length range than Great Lakes animals in spring, such a broad length range during June–August seems unlikely. Further data are required before either the 2.5- or 1.5-yr growth pattern could be considered to be convincingly demonstrated. It is noteworthy, however, that Hardisty and Potter (1971), based on interspecific comparisons, proposed that all the large anadromous parasitic lamprey species, which include *P. marinus*, have a juvenile period of at least 2.5 yr.

The size of sea lampreys found parasitizing anadromous species in rivers is likely a function of the size distribution of these teleost hosts. Potter and Beamish (1977) pointed out that survival from sea lamprey attack is related to size of both parasite and host and suggested that an ecological balance has been reached in natural river systems which would make high mortality of host populations unlikely. They further observed that the reduced size at maturity of landlocked sea lampreys would have been of great selective advantage due to the low density of teleosts of sufficient size to support larger sea lampreys. It would seem reasonable to extend this logic to the marine situation and imply that the larger the sea lamprey the larger would be a suitable host. In rivers, sea lampreys 15–40 cm in length parasitize primarily alewife, shad, and salmon which are approximately 25–30, 45–50, and 50–85 cm in length, respectively, during their spawning runs (F. W. H. Beamish 1980; Scott and Scott 1988). The largest of these sea lampreys were most commonly reported in association with salmon, the largest host species (F. W. H. Beamish 1980). Bigelow and Schroeder (1948, 1953) list marine hosts as including, in addition to the same anadromous species as observed in rivers, a number of entirely marine species which are common off Nova Scotia: cod, haddock, pollock (*Pollachius virens*), hake (*Urophycis* spp.), mackerel, basking shark, and swordfish. Present records add Atlantic herring and bluefin tuna to that list and give the first indications of the size of sea lampreys involved in some of these attacks (Table 2). Since herring and mackerel are generally less than 40 cm long and the groundfish cod, haddock, pollock, and hake are mostly less than 70–80 cm, it seems likely that attacks on these species are also by small sea lampreys. The records of sea lampreys 25–30 cm in length attached to a basking shark and a swordfish indicate, however, that small sea lampreys do not restrict their attacks to small-bodied hosts. If parasitism of groundfish is an important feature of sea lamprey behaviour, it would seem most likely to occur in the winter and spring months when the benthic shelf distribution of small sea lampreys places them in the vicinity of groundfish concentrations.

The pelagic distribution of large sea lampreys along the shelf edge and over the continental slope is clearly not consistent with feeding on demersal species. Potential prey which meet these distributional criteria and which are of sufficient size to sustain attacks by large sea lampreys are marine mammals and large pelagic fishes. Concentrations of whales, particularly sei and fin, commonly occur along the shelf edge, as well as on the shelf, in warmer months (Sutcliffe and Brodie 1977). Similarly sharks, swordfish and tunas and other less common large oceanic fishes occur in this area in summer and autumn (Scott and Scott 1988; IOP, unpubl. data). Wounds on the skin of these large pelagic animals are common. Although some proportion of these are attributable to the shark *Isistius brasiliensis* (Jones 1971), and this has caused some confusion in the literature, it is nonetheless clear that wounds caused by lampreys are frequent. Pike (1951) and van Utrecht (1959) described lamprey scars on various whale species and, as already noted, lamprey scars are particularly common on sei whales observed off Nova Scotia (P. Brodie, pers. comm.). Captures of sea lam-

preys attached to basking shark, swordfish, and bluefin tuna hosts (Table 2) and the scarring of swordfish reported by W. B. Scott (pers. comm.) also lend support to the importance of these species as hosts for sea lampreys. Nonetheless, there are no recorded direct observations of large sea lampreys actually attached to any of these species. However, P. W. G. McMullon (DFO Biological Station, St. Andrews, N.B.), who took the photographs of scars on swordfish which are in the St. Andrews Biological Station collection, recalls (pers. comm.) that these scars were typically "1.5–2 in." (38–51 mm) in width. Scars of this diameter would be consistent with parasitization by sea lampreys greater than 45 cm (Lennon 1954). Thus there is observational, if indirect, support for the hypothesis that large pelagic animals are the primary hosts of large sea lampreys.

Observations of attachment of sea lampreys 25–30 cm in length to swordfish and basking shark (Table 2) indicate that the association of sea lampreys with large pelagic animals may begin early in the marine period. Such an association could explain the virtual absence of animals 36–55 cm in length in marine collections. Also, the survey of sea lamprey sizes in rivers by F. W. H. Beamish (1980) and extensive measurements of sea lampreys in the St. John River by Potter and Beamish (1977) indicate that animals in this size range seldom occur in rivers. This virtual absence of medium-sized sea lampreys in collections would suggest not only an association with large pelagic prey but a closer association than that of large sea lampreys which were available, apparently in free-swimming mode, to midwater trawling in autumn. A close association between sea lampreys and large pelagic hosts, particularly by those in the length range 36–55 cm, is equally plausible under either the 1.5- or 2.5-yr juvenile growth period hypotheses. In the case of the 2.5-yr growth pattern, it would be necessary to propose that the association persists through the sea lampreys' second sea winter to explain the absence of medium-sized animals in samples. As large pelagic species occur off Nova Scotia primarily in summer and autumn, sea lampreys associated with them would be transported out of the sampled area over winter.

The proposal made here for extensive pelagic, and possibly wide-ranging, habits in *P. marinus* is supported by observations on the distribution of other large anadromous parasitic lamprey species. It is particularly noteworthy that the *Geotria australis* which originate in South American rivers have been observed off the island of South Georgia in what is apparently their second juvenile year, a distribution pattern requiring migration or transport over distances up to 1900 km over oceanic depths (Potter et al. 1979). This lends some credence to the suggestion made above of comparable behaviour in *P. marinus*. Feeding studies of the Pacific lamprey (*Lampetra tridentata*) indicate that teleosts inhabiting midwater and surface layers are important hosts (R. J. Beamish 1980) as are various whales (Pike 1951), and *L. tridentata* has been caught in surface waters during high-seas gillnet fishing (Larkins 1964) and in midwater over slope depths (Hubbs 1967). Smaller anadromous lamprey species with a 1.5-yr juvenile period (Hardisty and Potter 1971) such as *Lampetra fluviatilis* (Tuunainen et al. 1980) and *Lampetra ayresi* (R. J. Beamish 1980) are also pelagic although in surface waters close to shore. Thus, pelagic marine habits are common to many, if not all, anadromous lamprey species.

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Effects of Biomass–Range Interactions on Catchability of Migratory Demersal Fish by Mobile Fisheries: An Example of Atlantic Cod (*Gadus morhua*)[1]

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Rose, G. A., and W. C. Leggett. 1991. Effects of biomass–range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 48: 843–848.

We used daily acoustic estimates of the abundance and range of a migratory demersal species, Atlantic cod (*Gadus morhua*), coupled with catch statistics from a mobile gillnet fishery in the northern Gulf of St. Lawrence, to verify two predictions of the Paloheimo–Dickie hypothesis: (1) that biomass and range of fish distributions are positive covariates and (2) that catchability (q) is negatively correlated with biomass and occupied range. Fishing power changed little during this study (1985–86) and was thus not a major cause of variation in q. The daily biomass (b) of cod surveyed on the fishing ground was significantly and positively correlated with the range occupied (a) in both 1985 and 1986 ($b = 86a^{1.05}$; $R^2 = 0.71$; $P < 0.05$). Local cod densities assessed at small scales (1 km) were relatively stable. Daily catchability was a negative multiplicative function of both biomass ($q = 0.095b^{-0.787}$; $R^2 = 0.70$; $P < 0.05$) and occupied range ($q = 0.003a^{-0.747}$; $R^2 = 0.56$; $P < 0.05$). The q–range relationship derived in 1986 was used to hindcast q in 1985. Hindcast and observed 1985 q's were significantly correlated ($r = 0.74$; $P < 0.05$).

Des estimations quotidiennes, produites par une technique acoustique, de l'abondance et de la distribution de la morue franche (*Gadus morhua*), une espèce démersale migratoire, conjuguées aux statistiques recueillies sur les prises d'une pêche au filet maillant du nord du Golfe Saint-Laurent, ont servi à vérifier deux prévisions obtenues suivant l'hypothèse Paloheimo–Dickie : 1) la biomasse et l'aire de distribution sont des co-variables aléatoires positives et 2) le potentiel de capture (q) est en corrélation négative avec la biomasse et l'aire occupée. La puissance de pêche ayant très peu varié durant cette étude (1985–1986), elle n'est pas au nombre des principales causes de variation de la valeur de q. La biomasse quotidienne (b) de morues relevée dans la pêche était en corrélation significative et positive avec l'aire occupée (a) tant en 1985 qu'en 1986 ($b = 86a^{1.05}$; $R^2 = 0{,}71$; $P < 0{,}075$). La densité locale de morues évaluée à petite échelle (1 km) était relativement stable. Le potentiel de capture quotidien était une fonction multiplicative négative autant de la biomasse ($q = 0{,}095b^{-0.787}$; $R^2 = 0{,}70$; $P < 0{,}05$) que de l'aire occupée ($q = 0{,}003a^{-0.747}$; $R^2 = 0{,}56$; $P < 0{,}05$). On s'est servi de la relation q-aire déterminée en 1986 pour estimer rétrospectivement la valeur de q de 1985. On a constaté une corrélation significative entre le q de 1985 observé et la valeur estimée rétrospectivement ($r = 0{,}74$; $P < 0{,}05$).

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The use of commercial catch statistics to estimate stock abundance typically assumes constancy of catchability (q) over a range of catch rates and ecological and behavioral conditions (Garrod 1977). Violations of this assumption can lead to severe miscalculations of overall stock size, especially when abundances are low or declining (Baranov 1918; Paloheimo and Dickie 1964; Gulland 1964; Ricker 1977).

The theoretical basis for the nonconstancy of q is well established for mobile cooperative fisheries exploiting pelagic shoaling species (Paloheimo and Dickie 1964; Rothschild 1977). An increasing number of empirical studies have confirmed this expectation (MacCall 1976; Ulltang 1980; Winters and Wheeler 1985; Crecco and Savoy 1985). Moreover, variable q's are almost certain to characterize fisheries exploiting demersal and other species (Peterman and Steer 1981; Bannerot and Austin 1983). This is especially likely when vessels are highly mobile and fish exhibit aggregative behavior (e.g. Rose and Leggett 1989a). Several empirical studies have confirmed this expectation (Pope and Garrod 1975; Houghton and Flatman 1981; Crecco and Overholtz 1990).

Two key mechanisms have been hypothesized to account for the variance in q: (1) changing fishing power of commercial vessels (Gulland 1964) and (2) positive correlation between biomass and occupied range coupled with cooperative nonrandom fishing (Paloheimo and Dickie 1964). Attempts to conduct independent tests of these hypotheses have been problematic because fishing power changes, especially over long time periods, have been difficult to quantify. Moreover, the lack of independent estimates of biomass and range, especially for demersal species, has often precluded tests of the interaction of q with these factors (e.g. Pope and Garrod 1975; Houghton and Flatman 1981). In the few studies wherein biomass and range have been independently estimated (e.g. Crecco and

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Overholtz 1990), cooccurring temporal changes in fishing power and fish distribution and biomass have confounded direct inferences about their independent effects on q.

In this paper, we tested the fundamental tenets of the Paloheimo–Dickie (1964) hypothesis, independent of major changes in fishing power. We did this by assessing the daily biomass and range of migrating Atlantic cod (*Gadus morhua*) (employing fisheries acoustics methods) on the fishing grounds of a monitored mobile gillnet fleet. Specifically, we tested two hypotheses: (1) that biomass and the range occupied by cod would be positively correlated (and proportional) and (2) that q would be negatively correlated with both biomass and the range occupied. We then used a model based on these relationships, derived in a single year, to hindcast q in a year for which independent measures of cod range and q were available.

Methods

This study was conducted at Brador Bay (51°25′N, 57°15′W) in the northern Gulf of St. Lawrence in July 1985 (covering the central part of the gillnet fishery in that year) and from mid-June to early August 1986 (the full period of the gillnet fishery). The study area was delimited by the extent of the fishing grounds of the fleet under study (based at four villages: Blanc-Sablon, Lourdes-de-Blanc-Sablon, Brador, and Middle Bay). The grounds encompassed approximately 250 km^2 and spanned 30 km of coastline. This fishery exploits migrating cod of the northern Gulf stock (NAFO 3Pn4RS). These Gulf cod frequent the fishing grounds of Brador Bay in spring and summer in search of their capelin (*Mallotus villosus*) prey. Further details of the study area, the distributions of cod and capelin, and the dynamics of the fisheries at Brador Bay are given in Rose and Leggett (1988a, 1988b, 1989a, 1989b, 1990).

The gillnet fleet monitored in 1986 comprised 25 vessels fishing large-mesh (>14 cm) monofilament gillnets (90 × 3.6 m). Catches of each vessel were documented daily. Catches from the few additional vessels that fished in the area on a part-time basis were not included in our analyses. In 1985, catch rates from an average of 16 randomly selected vessels were monitored each day. During midseason (late June to late July), most of the fleet fished each day. However, prior to the beginning and after the end of the period of maximum catches, effort was reduced. The number of nets fished daily per boat averaged 20 and did not differ significantly between 1985 and 1986. Effort is therefore reported as cod weight (kilograms) per boat per day.

The biomass of cod present in the study area was assessed daily using the methods of fisheries acoustics (Mitson 1983). An average of 50 acoustic transects (1 km each) were run during daylight hours each day. The overall survey design was systematic and fixed. Transects were run across the study area in zigzags designed to sample all spatial and depth ranges. Precise transect bearings were initially chosen at random. Vessel speed was 10 km/h. Cod densities for each kilometre were determined by echo integration techniques (see Burczynski 1982). Relative integrator values were scaled by an estimate of the average backscattering cross-section of cod (0.002973 m^2) measured in situ using dual-beam techniques (Rose and Leggett 1988c). Cod were discriminated from other species commonly occurring in the study area (capelin and mackerel (*Scomber scombrus*)) by employing the acoustic backscattering classification methods developed for that purpose by Rose and Leggett (1988c). The area occupied by cod was defined as the percentage of transects containing acoustic signal strength equivalent to more than 10 average-sized cod (50 cm). This threshold was judged to be the lowest density at which a transect could be considered to be "occupied" by cod, relative to both the overall biomass and fishable concentrations for the gillnet fleet. Occupation rates calculated using a lower threshold (1 cod/km) exhibited a temporal pattern similar to those observed using the higher threshold.

The catchability of cod (q) was estimated daily as $q = C \cdot B^{-1} \cdot f^{-1}$ where C = catch, B = biomass, and f = effort.

Standard linear and stepwise regression techniques were employed in these analyses. Prior to entry into a model, variables were log transformed to standardize variances. Statistical analyses employed the programs of SAS for personal computers (SAS Institute, Cary, NC) and STATGRAPHICS (Statistical Graphics Corp., Rockville, MD). Significance was declared if $P < 0.05$.

Results

The total biomass of cod surveyed daily within the study area ranged from approximately 10 to 5000 t in 1986 and to over 10 000 t in 1985 (Fig. 1). The area occupied ranged from <10 to approximately 40% of the overall study area in both 1985 and 1986. The relationships between biomass and area did not differ significantly between years. For the pooled data, biomass (b) was significantly and positively correlated with the percentage of the range occupied (a) ($b = 86.5a^{1.05}$; SE (slope) = 0.09; df = 61; $R^2 = 0.71$). The slope of this relationship did not differ significantly from 1 (t-test), indicating that the relationship between biomass and range was proportional over the range of available data. Residuals were neither significantly autocorrelated nor correlated with the predicted values.

The daily catchability (q) of cod varied over several orders of magnitude in 1986 (Fig. 2) and in 1985 (Fig. 5). A lack of any significant autocorrelation in the q time series indicated that variance did not occur at fixed frequencies.

Daily catchability was significantly and negatively correlated with the range occupied (a) by cod in 1986 ($q = 0.003a^{-0.747}$; SE (slope) = 0.11; df = 38; $R^2 = 0.56$) (Fig. 3). Residuals were neither significantly autocorrelated nor correlated with predicted values. Catchability was also significantly and negatively correlated with cod biomass (b) assessed daily ($q = 0.095b^{-0.787}$; SE (slope) = 0.08; df = 38; $R^2 = 0.70$) (Fig. 4). Residual autocorrelation was significant ($r = 0.51$) only at a lag of 1 d. Correlation with predicted values was not significant.

To test the reliability of the relationship between q and the distribution of cod, the model of q based on the range occupied by cod in 1986 was used to hindcast daily q documented independently in 1985 (Fig. 5). Range rather than biomass was used as the predictor of q because q was estimated independently of range (q was not estimated independently of biomass). The hindcast levels of q and those observed in the fishery in 1985 were significantly and positively correlated ($r = 0.74$). The slope of this relationship (0.75; SE = 0.17, df = 17) differed significantly from 1 (the value indicating that the observed and predicted values were proportional).

Discussion

Our data verified the predictions of the Paloheimo–Dickie (1964) hypothesis for a mobile cooperative fishery exploiting a demersal migratory species, Atlantic cod. As predicted, fish

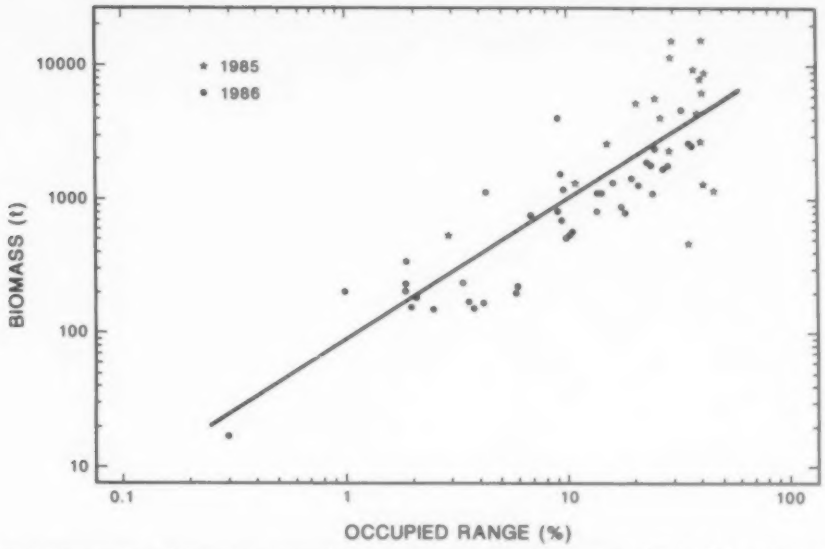

FIG. 1. Regression of biomass on occupied range (% of total fishing ground, 250 km^2) for migratory cod at Brador Bay in 1985 and 1986 (biomass = 86.5 × range$^{1.05}$; SE (slope = 0.09; df = 61; R^2 = 0.71).

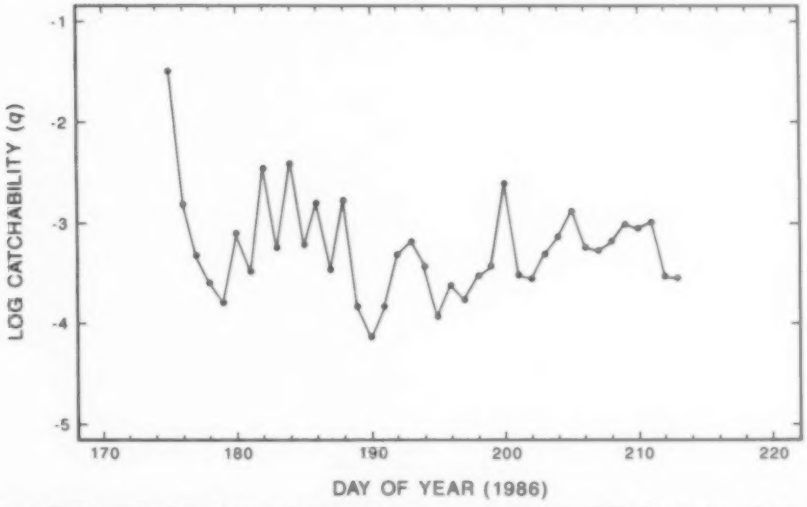

FIG. 2. Daily catchability of the cod gillnet fishery at Brador Bay in 1986. The series exhibits no significant autocorrelation ($P > 0.05$).

biomass was positively correlated with the range occupied (Fig. 1). Moreover, biomass and range were proportional (slope = 1) over the range of values observed in two seasons of study. This result suggested that at small scales (kilometres), during the nearshore summer feeding period, the densities of cod aggregations remained remarkably stable and independent of larger scale biomass (abundance). It is noteworthy that constant (and high) local aggregation densities are consistent with theory on the food-finding function of shoaling behavior (Pitcher 1986). Moreover, stable small-scale densities have been predicted from studies of feeding-based production processes scaled to body size (Boudreau and Dickie 1989). It follows that cod migrating onto the inshore fishing grounds occupied range additional to that already occupied by earlier migrants (at least up to the limits of the favorable habitat). In keeping with these findings, local maximum densities of cod have been shown to remain relatively constant while fish are inshore at Brador Bay (Rose and Leggett 1989b).

Our data also verified the hypotheses that catchability (q) would vary from day to day relative to the changing biomass of migrating cod (Fig. 4) and to the changing range occupied by these fish (Fig. 3 and 5) (the implied precision of the q–biomass correlation is predictably somewhat stronger than the q–range correlation, given that q was calculated as catch rate/biomass). This result is consistent with previous findings at Brador Bay that stable catch rates of the gillnet fishery (relative to those of the trap fishery) can be accounted for to a large extent by the constancy of densities at which cod tend to aggre-

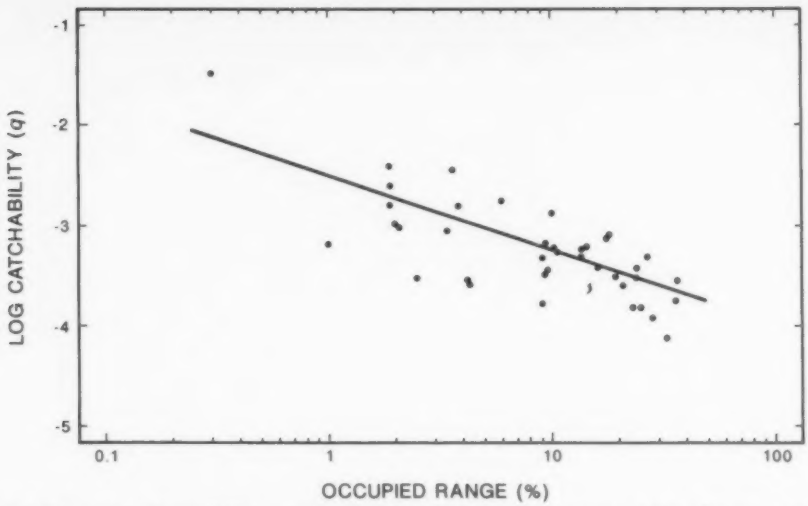

FIG. 3. Regression of catchability on occupied range (% of total fishing ground, 250 km^2) for the gillnet fishery exploiting cod at Brador Bay in 1986 ($q = 0.003 \times \text{range}^{-0.747}$; SE (slope) = 0.11; df = 38; $R^2 = 0.56$).

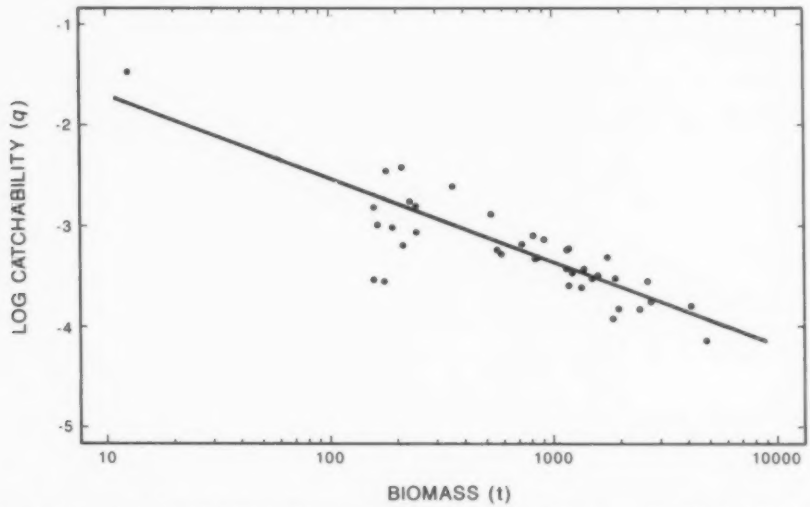

FIG. 4. Regression of catchability on biomass of cod for the gillnet fishery at Brador Bay in 1986 ($q = 0.095 \times \text{biomass}^{-0.787}$; SE (slope) = 0.08; df = 38; $R^2 = 0.70$).

gate in this nearshore environment and the effectiveness with which fishermen locate these cod aggregations (Rose and Leggett 1989a). Catch rates in gillnet fisheries in Norway have also been shown to be dependent on cod densities at small scales adjacent to the nets (Dickson 1989).

We believe that the underlying causes of the consistent relationships demonstrated between catch rates, catchability, density, biomass, and range (both in this and other studies) are to be found in the relative behavior of fish and fishermen. Cod aggregations are highly mobile, as are cod gillnet fishermen. Cod respond quickly to changes both in the nearshore physical environment (temperatures, currents, salinities) and to the distribution of their capelin prey (Rose and Leggett 1988a, 1988b, 1989a, 1989b, 1990). Fishermen in turn respond to the dynamics of fish distribution by actively searching for and tracking these mobile fish aggregations. Once an aggregation is located, effort is concentrated at that location until the fish move again (Rose and Leggett 1989a). Hence, catch rates are determined not only by density factors but also by the abilities of fishermen to learn and exploit fish aggregative properties and behavior and by the extent to which this information is shared within the fishing fleet.

The significant correlation between q's predicted by the 1986 q–range function and those independently observed in 1985 indicates that the interaction between fish distribution and fishing success was similar in the two years studied. However, the tendency for 1985 observed q's to be somewhat less than those predicted suggests that fishermen may have improved their fishing tactics to some degree between 1985 and 1986. We believe that this may have been a consequence of our acoustic

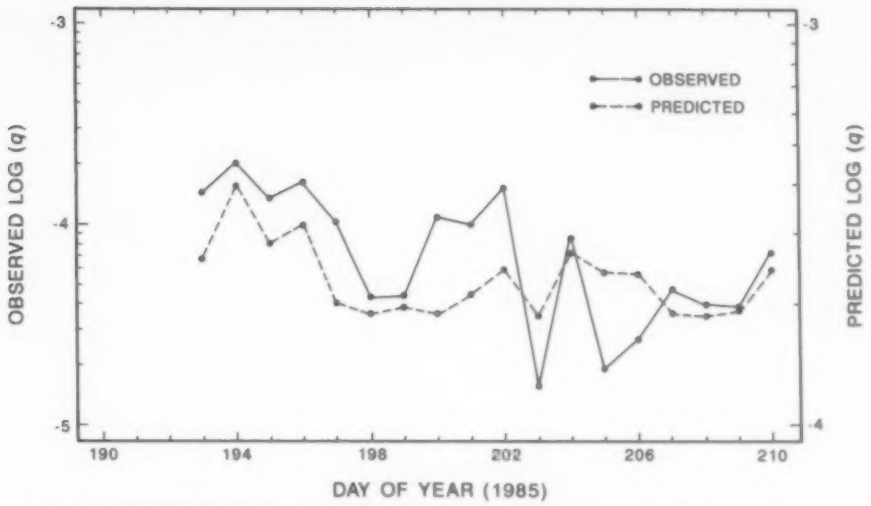

FIG. 5. Observed and predicted catchability in the cod gillnet fishery at Brador Bay in 1985. Predictions are based on the regression model derived in 1986 employing occupied range as the independent variable ($q = 0.003 \times \text{range}^{-0.747}$). Observed and predicted values are significantly correlated ($r = 0.74$; slope = 0.75; SE (slope) = 0.17; df = 17).

surveys, the results of which were discussed with fishermen at dockside on an informal basis. We noted that during 1986, fishermen were more inclined to use this information than in 1985.

These interactions between mobile fish and fishermen suggest that for species exhibiting aggregative behavior, catch rates will tend to remain relatively stable (or at least independent of fish biomass), except in cases where fish aggregations can no longer be located in sufficient number and size to saturate fishing capacities. This conclusion, drawn here from observations of an inshore gillnet fishery for cod, is consistent with Templeman's (1966) observations on the offshore wintertime cod fishery that as stocks decline under heavy fishing pressure, the remaining fish will "form a school in a smaller and smaller area, and the school will still be vulnerable to heavy fishing when it is found. In this case there would still be good deepwater trawling in winter and spring until the stock has been greatly reduced."

Our data demonstrate that q is correlated with both fish biomass and range at small spatial (kilometres) and temporal (days) scales. We believe that the relationships demonstrated at these small scales will also hold at larger scales and with other demersal species. For example, Crecco and Overholtz (1990) have shown that at scales assessed in years and whole stock range, the q of haddock (*Melanogrammus aeglefinus*) was inversely related to both the biomass of the stock and the occupied range. For other cod fisheries, q has been shown in several instances to be inversely related to stock size (Pope and Garrod 1975; Houghton and Flatman 1982; Cook and Armstrong 1985). The consistencies among the above results (at various scales and with different demersal species) and our present findings, coupled with the more ample evidence from pelagic fisheries (reviewed by Winters and Wheeler 1985), provide strong evidence of the generality of the theoretical predictions of Paloheimo and Dickie (1964), both to pelagic and demersal species.

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Changes in Habitat and Microhabitat Partitioning within an Assemblage of Stream Fishes in Response to Predation by Sacramento Squawfish (*Ptychocheilus grandis*)

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Brown, L. R., and P. B. Moyle. 1991. Changes in habitat and microhabitat partitioning within an assemblage of stream fishes in response to predation by Sacramento squawfish (*Ptychocheilus grandis*). Can. J. Fish. Aquat. Sci. 48: 849–856.

The Sacramento squawfish (*Ptychocheilus grandis*), a piscivorous cyprinid, was recently (ca. 1979) introduced into the Eel River, California, USA. We compared habitat and microhabitat use of resident fishes between areas where squawfish were present and absent at one location and between years before and after invasion by squawfish at a second location. The resident species showed a variety of responses to the presence of the predator. Juvenile rainbow trout (*Oncorhynchus mykiss*) and juvenile Sacramento suckers (*Catostomus occidentalis*) increased their use of fast-flowing riffles at both locations, in the presence of squawfish. Suckers also used significantly shallower depths within habitat types. Adult California roach (*Lavinia symmetricus*) decreased their use of run habitat and increased use of pools and riffles at the first site, but not at the second. When squawfish were present, juvenile roach and threespine stickleback (*Gasterosteus aculeatus*) were found in shallower water closer to the stream edge in all habitats. Spatial overlaps tended to be lower in the presence of squawfish. The introduction of squawfish has resulted in changes in the habitat and microhabitat use of the resident fish assemblage but no loss of species.

La sauvagesse du Sacramento (*Ptychocheilus grandis*), cyprinidé piscivore, a été récemment introduite (vers 1979) dans la rivière Eel, en Californie. Nous avons comparé l'utilisation de l'habitat et du microhabitat des poissons résidants entre des secteurs où les sauvagesses étaient présentes et absentes, en un point, et entre les années avant et après l'invasion par les sauvagesses, en un deuxième point. Les espèces résidantes réagissent de façon très variable à la présence du prédateur. Les juvéniles de truite arc-en-ciel (*Oncorhynchus mykiss*) et de meunier du Sacramento (*Catostomus occidentalis*) ont, en présence de sauvagesses, augmenté leur utilisation des radiers à courant rapide aux deux endroits. Les meuniers utilisaient aussi des profondeurs nettement plus faibles parmi les divers types d'habitats. Les adultes de *Lavinia symmetricus* ont diminué leur utilisation des parcours et augmenté celle des fosses et des radiers au premier site, mais pas au deuxième. En présence des sauvagesses, les jeunes de *Lavinia* et d'épinoche à trois épines (*Gasterosteus aculeatus*) se retrouvaient en eau moins profonde, plus près du rivage, dans tous les habitats. Les chevauchements spatiaux étaient généralement plus faibles en présence des sauvagesses. L'introduction des sauvagesses a provoqué des modifications dans l'utilisation de l'habitat et du microhabitat par l'assemblage de poissons résidants, mais n'a causé aucune disparition d'espèces.

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Behavioral studies have shown that some stream fishes exhibit major changes in habitat use in the presence of predatory fish, typically selecting shallower or more structurally complex portions of the habitat (Cerri and Fraser 1983; Fraser and Emmons 1984; Power et al. 1985; Fraser and Gilliam 1987; Schlosser 1987). Power (1984) suggested that the distribution of armored catfishes in a Panama stream was the result of balancing the threat of fish predators in deep water with that of avian predators in shallow water. These studies indicate that patterns of spatial segregation observed in assemblages of stream fishes are partially the result of predation.

In 1979 or 1980, the Sacramento squawfish (*Ptychocheilus grandis*), a piscivorous cyprinid, was illegally introduced into the Eel River, a large coastal drainage in California, USA. Squawfish (i.e. Sacramento squawfish) spread rapidly through the Eel River drainage but have not invaded all suitable areas (L. R. Brown and P. B. Moyle, unpubl. data). Diet data from the Eel River (unpubl.) and other areas of California (Moyle 1976; Brown 1991) indicate that all of the fishes present in the Eel River are eaten by squawfish. We have treated the invasion as a natural experiment in two ways. First, we compared the use of habitat (pool, riffle, run) and microhabitat (depth and water velocity at positions within a habitat) by the resident fish assemblage in similar areas with and without squawfish. Second, we compared the use of habitat and microhabitat by the resident fishes in the same area, before and after the invasion by squawfish.

Study Sites and Methods

We conducted the study comparing habitat and microhabitat use between similar areas in the South Fork of the Eel River, Mendocino and Humboldt counties, California. As in other California coastal streams, flow is highly seasonal with peaks in winter and low summer discharge. The native resident species were Sacramento sucker (*Catostomus occidentalis*), rain-

bow trout (*Oncorhynchus mykiss*), threespine stickleback (*Gasterosteus aculeatus*), and Pacific lamprey (*Lampetra tridentata*). The California roach (*Lavinia symmetricus*) was introduced around 1970 and is now the most abundant species in the system. The present assemblage is a common one in California coastal stream (Moyle 1976). As of 1988, squawfish were abundant in the South Fork Eel River up to Benbow Reservoir (40°03′N, 123°47′W, elevation = 111 m), near Garberville. We chose three sites downstream of Garberville to characterize the microhabitat use of fishes in the presence of squawfish. We chose three sites upstream of Benbow Reservoir to characterize the microhabitat use of the resident fishes in the absence of squawfish. We attempted to select physically similar sites in both areas. The pools selected were uniform in shape with one bank gently sloping into deep water and the other bank falling steeply into deep water. Substrate was dominated by detritus, primarily senescent algae, and gravel. Cover was limited to boulders, overhanging vegetation, and logs located along the deep edge of the pool. Substrate in riffles and runs was dominated by detritus and gravel, with some cobble also present. Cover was provided by the substrate and surface turbulence. Rainbow trout were rare during this study due to mortalities which occurred in early August 1988 when water temperatures exceed 29.0°C.

We conducted the comparison of habitat and microhabitat use before and after invasion by squawfish in the Van Duzen River, a major tributary to the Eel River. The seasonal flow regime is similar to that of the South Fork Eel River. The resident species were the same as in the South Fork Eel River except for a few speckled dace (*Rhinichthys osculus*), another recently introduced species. The sites in this study were located near Bridgeville (40°29′N, 123°50′W, elevation = 183 m). In July and August 1987, we documented microhabitat use by resident fishes before the invasion of squawfish. We studied microhabitat use by resident fishes in the presence of squawfish in September 1989. We did not observe squawfish during snorkel surveys of the area in October 1988 (unpubl. data), indicating that the site was invaded sometime between October 1988 and September 1989. The pools were less regular in shape than those surveyed in the South Fork Eel River. Deep water occurred in isolated pockets near boulders or bedrock formations rather than a single continuous area. The boulders and bedrock were the primary cover available. Substrate was primarily gravel and sand. The substrate of riffles and runs was dominated by boulders and cobble. Cover was provided by the substrate and surface turbulence.

We made microhabitat observations on undisturbed fishes by snorkeling in an upstream direction. Fishes were considered undisturbed if they exhibited "normal" behavior, neither approaching nor avoiding the diver. Once a fish was located, it was identified to species and its standard length (SL) estimated (± 5 mm) by comparison with substrate elements, which were measured with a wading rod. Observations on more than one individual (i.e. schools) were treated as a single datum. We also characterized the habitat for each observation as pool, riffle, or run.

For each fish, we recorded the following measurements: (1) total depth; (2) mean water column velocity; (3) distance to the edge of the stream; and (4) width of the stream. Depth was measured to the nearest centimetre using a wading rod. Water velocity (centimetres per second) was measured with a Marsh–McBirney model 201 electronic flowmeter. We calculated mean water column velocity as the velocity at 0.6 of the water column depth when depth was less than 75 cm or the mean of measurements at 0.2 and 0.8 of the water column depth in deeper water. In areas of turbulent flow, a weighted mean was calculated from all three proportional depths (Bovee and Milhous 1978). Distance to the edge of the stream (metres) and stream width (metres) were used to calculate the proportional distance of each fish between the shore and midstream by dividing the distance from the closest edge by one-half the total width (range 0.0–1.0, referred to as "distance to edge" for the remainder of this paper). This measure was used rather than the measured distance to edge (metres) because it takes into account the variation in width within and among habitat types.

We divided the data for most species into two size-classes, based on the first break in length frequency histograms. Sacramento squawfish and rainbow trout were separated at 120 mm SL, Sacramento sucker at 110 mm SL, and California roach at 50 mm SL. All threespine stickleback observed were less than 40 mm SL.

In the South Fork Eel River, we also compared counts of fish in 1-m^2 quadrats from the two areas. At each of our six sampling sites, we marked five quadrats at each of three depths (25, 50, and 100 cm). We positioned the quadrats randomly along a transect parallel to the stream located on the shallow, sloping side of the pool. Counts were made by a single diver who approached each quadrat from the center of the pool. Counts were made after the detritus disturbed by quadrat placement had settled (approximately 30 min after placement of the last quadrat). All fish in a quadrat were identified to species and counted.

We collected data on microhabitat availability to determine if direct comparisons of the fish microhabitat data between areas (South Fork Eel River) or years (Van Duzen River) were justified. At each site, we divided the reach of stream where microhabitat data were collected into 20-m sections. Within each 20-m section, we randomly positioned a single transect using an electronic random number generator. At that point, we placed a transect line across the stream, perpendicular to the direction of flow, and measured total depth and mean water column velocity at 10 evenly placed points along the transect.

We compared availability of total depth, availability of mean water column velocity, and microhabitat use data between areas (or years) with t-tests. Depth and velocity data were $\ln(x+1)$ transformed and distance to edge was angular transformed because of heterogeneity of variances in the original data (Bartlett's test, Sokal and Rohlf 1981). Data from sites within areas (e.g. the three sites in the South Fork Eel River where squawfish were present) were pooled because habitat availability and microhabitat use within the area were the variables of interest.

We compared the total number of availability observations made in each habitat type (pool, riffle, or run) in the two areas of the South Fork Eel River to determine if we were successful in selecting physically similar areas. Riffles and runs were not distinguished in some of the 1987 Van Duzen River data, so we compared availability of habitat on the basis of two habitat types, pool and riffle/run.

In the South Fork Eel River, we divided data into pool observations and riffle/run observations for sticklebacks, roach adults, and roach juveniles. Data on juvenile trout and suckers were not stratified by habitat because these species were absent from pools where squawfish were present. In the Van Duzen River, we analyzed all species by habitat. Stickleback data were not analyzed because this species was restricted to the lowermost sampling site by a barrier. Speckled dace data were not

analyzed because this species was recently introduced and was only present at the uppermost sampling site.

We compared the South Fork Eel River quadrat data between areas with a chi-square test. We pooled the total numbers of fish observed in quadrats for each depth in areas with and without squawfish. Parametric statistics were not appropriate because at some sites where squawfish were present, all counts at deeper quadrats were zero.

We calculated spatial overlaps between all of the species for total depth, mean velocity, and distance to edge. Overlaps were calculated using Schoener's (1970) overlap measure:

$$S = 1 - 0.5(\Sigma |P_{x,i} - P_{y,i}|)$$

where $P_{x,i}$ and $P_{y,i}$ are the proportions of the resource i used by species x and y. Values range from 0.0 (no overlap) to 1.0 (complete overlap). We separated depths, velocities, and distance to edge into categories by units of 10 (e.g. 1–10 cm, 0–10 cm·s^{-1}, and 0.0–0.1, respectively) for the calculations. If data were sparse, we pooled categories until cells contained a minimum of five observations. We arbitrarily designated a value of ≤ 0.33 as low overlap and a value of ≥ 0.67 as high overlap. We arbitrarily chose a difference of 0.1 as worthy of mention. The 0.1 value does not imply statistical significance. We calculated the overlaps because the results illustrated the effects that differences in the habitat and microhabitat use of the species in the presence of squawfish had on the spatial interrelationships among the species. We felt that using overlaps to link the species was conceptually useful and gave an overall view of the response of the fish assemblage to the presence of squawfish, despite the lack of any statistical rigor in our use of the overlap measure.

Results

Habitat and Microhabitat Availability

The proportion of observations made in runs, riffles, and pools did not differ between areas in the South Fork Eel River ($P > 0.05$), indicating that we successfully chose physically similar study sites. In the Van Duzen River, the proportion of observations made in pools and riffle/run differed between years ($P < 0.05$), indicating that the availability of habitat varied between years at the study site.

Availability of total depth was not significantly different between areas in the South Fork Eel River or between years in the Van Duzen River (Table 1). Mean water column velocity did not vary between areas in the South Fork Eel River but was different between years in the Van Duzen River (Table 1). Mean water column velocity in pools was 7.9 ± 4.9 (SD) cm·s^{-1} in 1987 and 1.8 ± 1.7 cm·s^{-1} in 1989 ($t = 14.8$, df = 291, $P < 0.001$) and in riffles was 15.1 ± 16.2 cm·s^{-1} in 1987 and 14.1 ± 21.0 cm·s^{-1} in 1989 ($t = 2.2$, df = 252, $P = 0.028$; transformation did not equalize variances in this case). We felt that the statistically significant difference of 1 cm·s^{-1} in riffle/run was more indicative of the large sample size involved (high statistical power) than biologically significant differences in availability; however, the more substantial difference in pools would probably affect comparisons of microhabitat use data.

To determine if the difference in availability of water velocities in pools could influence depth selection of fishes in the Van Duzen River, we calculated the Pearson product–moment correlation between depth and velocity for the 1987 availability data. In 1989, all velocities were less than 10 cm·s^{-1}. The correlation was not significant ($r = 0.07$, df = 103, $P > 0.05$). A plot of the data showed that velocities >10 cm·s^{-1} occurred (23 of 92 observations) at depths ≤70 cm, but velocities ≤10 cm·s^{-1} were more common (59 of 92 observations). Further, all depths >70 cm had velocities <10 cm·s^{-1}. Thus, fish could select depth independent of high velocity, and comparisons of total depth between years were appropriate. We did not compare mean water column velocities used by fish in pools between years because of the large difference in availability.

Habitat Use

In the South Fork Eel River, we found significant differences in habitat use for adult roach, rainbow trout, and suckers (Table 2). In the presence of squawfish, adult roach used run habitat less often and used riffle and pool habitat more often. Juvenile trout and suckers used pool habitat less often and riffle habitat more often.

TABLE 1. Physical characteristics of sample sites. Values are means (± SD) and sample sizes are given in parentheses. Depths and mean water column velocities were compared between areas (South Fork Eel River) or times (Van Duzen River) with a t-test (NS = $P > 0.05$, ***$P < 0.001$). Statistical tests were performed with $\ln(x+1)$ transformed data.

	South Fork Eel River		Van Duzen River	
Variable	Squawfish present	Squawfish absent	Squawfish present	Squawfish absent
Depth (cm)	62 ± 57 NS (349)	63 ± 59 NS (250)	40 ± 39 NS (326)	32 ± 26 NS (221)
Mean water column velocity (cm·s^{-1})	9 ± 16 NS (349)	8 ± 14 NS (250)	7 ± 15*** (326)	12 ± 13*** (221)
Flow (m^3·s^{-1})	0.54 ± 0.15 (23)	0.54 ± 0.15 (23)	0.24 ± 0.06 (8)	0.42 ± 0.09 (14)
Width (m)	20.0 ± 6.8 (35)	19.0 ± 9.7 (25)	16.2 ± 8.2 (32)	10.8 ± 6.1 (23)
Distance surveyed (m)	660	483	638	456
Water temperature range (°C)	15.5–27.0	15.5–27.0	16.5–23.5	17.8–24.1

TABLE 2. Proportions of observations made in each habitat type for each species in areas with Sacramento squawfish present (P) and absent (A). Results of chi-square tests between areas are shown.

Species	Size-class	SQ	n	Pool	Riffle	Run
Threespine stickleback	All	P	92	0.66	0.09	0.25
		A	220	0.64	0.10	0.26
		$\chi^2 = 0.1$, df = 2, $P = 0.93$				
California roach	Juvenile	P	271	0.63	0.11	0.26
		A	200	0.59	0.13	0.28
		$\chi^2 = 0.9$, df = 2, $P = 0.65$				
	Adult	P	67	0.45	0.31	0.24
		A	40	0.33	0.17	0.50
		$\chi^2 = 7.9$, df = 2, $P = 0.02$				
Rainbow trout	Juvenile	P	9	0.00	0.78	0.22
		A	34	0.41	0.41	0.18
		$\chi^2 = 5.5$, df = 1, $P = 0.02$[a]				
Sacramento sucker	Juvenile	P	9	0.00	0.89	0.11
		A	41	0.95	0.00	0.05
		$\chi^2 = 38.9$, df = 12, $P < 0.001$[a]				
Sacramento squawfish	Juvenile	P	39	0.67	0.15	0.18
	Adult	P	78	0.62	0.05	0.33

[a]For these two comparisons, riffle and run habitat were lumped. In both cases, expected cell frequencies of less than five occurred.

In the Van Duzen River, we found significant differences in the availability of habitat types between years, so we did not compare habitat use directly. Instead we examined changes in selection between years by comparing habitat use of each group with habitat availability using chi-square tests and comparing the results between years (Table 3). In 1987, all species groups used habitat in proportion to availability except juvenile suckers, which selected pool habitat. In 1989, when squawfish were present, juvenile suckers used habitat in proportion to availability, a decrease in use of pools compared with 1987. Rainbow trout juveniles avoided pool habitat in 1989. Juvenile roach selected pool habitat in 1989.

Microhabitat Use

In the South Fork Eel River, we found differences in microhabitat use between the two areas for all species (Table 4). In the Van Duzen River, all species except adult and juvenile rainbow trout exhibited differences between years. In the South Fork Eel River, sticklebacks and juvenile roach were found in shallower water in both habitat types, where squawfish were present. The same relationship was observed for adult roach in riffle/run habitat and juvenile suckers (pool and riffle/run habitats combined). These results were supported by the quadrat data (Table 5). In the Van Duzen River, juvenile roach and juvenile suckers were found in shallower water in both pools and riffle/runs, when squawfish were present (Table 4). In the South Fork Eel River, juvenile suckers, adult roach, and juvenile rainbow trout were found at significantly higher velocities where squawfish were present, reflecting increased use of riffles. In the Van Duzen River, adult roach in riffles used lower velocities when squawfish were present, but the diference was small and the change was in the direction expected, based on the small difference in availabilities. In the South Fork Eel River, sticklebacks (pools only), juvenile roach, and adult roach (riffle/run only) were found closer to the edge of the stream where squawfish were present.

Because of the widely differing sample sizes for the microhabitat comparisons, the statistical power of the comparisons varied widely. For example, in the South Fork Eel River the mean total depth of roach juveniles in pools differed by only 10 cm and was statistically significant (df = 285) but the mean total depth of rainbow trout juveniles differed by 21 cm and was not (df = 43). Also, the transformations failed to equalize variances for four comparisons (Table 4). The differences were highly significant or not significant in three cases but the comparison of total depth of juvenile California roach in Van Duzen River riffle/run was only significant at $P < 0.05$. The decline in total depth in the presence of squawfish should be treated with caution although the highly significant decline found in the South Fork Eel River for this comparison suggests that the change in the Van Duzen river was the result of a biological response.

Spatial Overlaps

In both streams, high overlaps were more common when squawfish were absent (Table 6). The changes in spatial overlap among the species pairs reflected changes in habitat use.

TABLE 3. Selection of habitat types for each species in 1989 (squawfish present) and 1987 (squawfish absent) in the Van Duzen River. Riffle and run habitats were lumped into a single category designated R/R. Results of chi-square tests between years are shown.

Species	Size-class	Year	n	Pool	R/R	χ^2	df	P
Habitat availability		1989	326	0.58	0.42	—	—	—
		1987	221	0.48	0.52	—	—	—
California roach	Juvenile	1989	322	0.67	0.33	6.1	1	0.013
		1987	138	0.50	0.50	0.2	1	NS
	Adult	1989	44	0.43	0.57	3.3	1	NS
		1987	79	0.46	0.54	0.1	1	NS
Rainbow trout	Juvenile	1989	99	0.08	0.92	75.1	1	<0.001
		1987	157	0.38	0.62	3.2	1	
	Adult	1989	27	0.63	0.37	0.3	1	NS
		1987	30	0.43	0.57	0.2	1	NS
Sacramento sucker	Juvenile	1989	63	0.57	0.43	<0.1	1	NS
		1987	28	0.71	0.29	5.7	1	0.017
Sacramento squawfish	Juvenile	1989	25	0.64	0.36	0.4	1	NS
	Adult	1989	37	0.97	0.03	22.1	1	<0.001

TABLE 4. Mean values (± SD) for the microhabitat variables total depth, mean water column velocity, and distance to edge (relative position between the edge and midstream, 0 = edge and 1 = midstream) for fishes of the South Fork Eel River in areas with Sacramento squawfish (SQ) present (P) and absent (A) and for fishes of the Van Duzen River in years with SQ = P and SQ = A. Habitat is divided into pool and combined riffle and run (R/R). The significance level for each *t*-test is shown below the values compared (NA = not applicable, NS = $P > 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Statistical tests were performed with $\ln(x + 1)$ (total depth and mean water column velocity) or angular transformed (distance to edge) data.

Species and habitat	*n*	SQ	Total depth (cm)	Mean water column velocity ($cm \cdot s^{-1}$)	Distance to edge
			South Fork Eel River		
Threespine stickleback (all)					
Pool	61	P	46 ± 23	2 ± 1	0.30 ± 0.24
	141	A	95 ± 52	3 ± 2	0.55 ± 0.27
			***[a]	NS	***
R/R	31	P	37 ± 32	10 ± 10	0.57 ± 0.27
	79	A	55 ± 37	12 ± 12	0.61 ± 0.25
			*	NS	NS
California roach juveniles					
Pool	170	P	69 ± 38	2 ± 1	0.33 ± 0.25
	117	A	79 ± 45	2 ± 2	0.44 ± 0.27
			*	NS	***
R/R	101	P	40 ± 32	13 ± 15	0.48 ± 0.26
	83	A	57 ± 38	12 ± 11	0.58 ± 0.27
			**	NS	*
California roach adults					
Pool	30	P	103 ± 49	2 ± 1	0.22 ± 0.23
	13	A	123 ± 43	2 ± 2	0.33 ± 0.20
			NS	NS	NS
R/R	37	P	42 ± 27	23 ± 19	0.65 ± 0.28
	27	A	89 ± 47	15 ± 16	0.47 ± 0.30
			**	*	*
Rainbow trout juveniles					
All	9	P	39 ± 25	44 ± 28	0.71 ± 0.25
	34	A	70 ± 55	19 ± 24	0.50 ± 0.32
			NS	*	NS
Sacramento sucker juveniles					
All	9	P	35 ± 29	42 ± 13	0.70 ± 0.17
	41	A	114 ± 47	2 ± 1	0.56 ± 0.25
			***	***	NS
Sacramento squawfish juveniles					
All	39	P	47 ± 31	11 ± 20	0.47 ± 0.25
Sacramento squawfish adults					
All	78	P	120 ± 53	8 ± 13	0.53 ± 0.29
			Van Duzen River		
California roach juveniles					
Pool	216	P	46 ± 28	2 ± 2	0.36 ± 0.29
	69	A	63 ± 35	8 ± 5	NA
			***[a]	NA	NA
R/R	106	P	29 ± 11	10 ± 8	0.52 ± 0.28
	69	A	32 ± 10	11 ± 9	NA
			**[a]	NS[a]	NA
California roach adults					
Pool	19	P	69 ± 23	6 ± 5	0.57 ± 0.26
	36	A	66 ± 31	10 ± 4	NA
			NS	NA	NA
R/R	25	P	30 ± 8	13 ± 7	0.55 ± 0.21
	43	A	34 ± 10	15 ± 9	NA
			NS	*	NA
Rainbow trout juveniles					
Pool	8	P	49 ± 14	2 ± 2	0.49 ± 0.18
	60	A	63 ± 23	9 ± 5	NA
			NS	NA	NA

TABLE 4. (*Concluded*)

Species and habitat	*n*	SQ	Total depth (cm)	Mean water column velocity ($cm \cdot s^{-1}$)	Distance to edge
R/R	91	P	30 ± 8	23 ± 19	0.62 ± 0.23
	97	A	31 ± 14	19 ± 13	NA
			NS	NS	NA
Rainbow trout adults					
Pool	17	P	100 ± 43	3 ± 3	0.45 ± 0.25
	13	A	102 ± 39	7 ± 5	NA
			NS	NA	NA
R/R	10	P	33 ± 8	18 ± 14	0.60 ± 0.33
	17	A	38 ± 9	21 ± 8	NA
			NS	NS	NA
Sacramento sucker juveniles					
Pool	36	P	30 ± 11	2 ± 4	0.28 ± 0.26
	20	A	66 ± 28	9 ± 5	NA
			***	NA	NA
R/R	27	P	27 ± 11	12 ± 9	0.53 ± 0.24
	8	A	53 ± 13	11 ± 5	NA
			***	NS	NA
Sacramento squawfish juveniles					
Pool	16	P	44 ± 22	1 ± 1	0.24 ± 0.23
R/R	9	P	36 ± 10	10 ± 7	0.63 ± 0.23
Sacramento squawfish adults					
Pool	36	P	115 ± 44	3 ± 2	0.50 ± 0.24
R/R	1	P	45	31	0.85

[a]Transformations failed to equalize variances for these comparisons.

TABLE 5. Depth distributions of juvenile California roach and threespine stickleback in areas with Sacramento squawfish present (P) and absent (A). Data are total number of juvenile California roach and threespine sticklebacks counted in five 1-m^2 quadrats at each of three depths 25, 50, and 100 cm) at three sites in areas with SQ = P and SQ = A.

	Depth		
SQ	25	50	100
Threespine stickleback			
P	16	11	0
A	24	53	26
$\chi^2 = 16.3$, df = 2, $P < 0.001$			
California roach juveniles			
P	221	126	20
A	57	50	25
$\chi^2 = 25.0$, df = 2, $P < 0.001$			

The largest declines in spatial overlap occurred when one member of a pair showed a strong habitat shift or when members of a pair exhibited opposite responses in the presence of squawfish. For example, overlap of juvenile rainbow trout with juvenile roach declined for all variables in both streams because of the strong shift of trout into riffles when squawfish were present. Conversely, the largest increases in spatial overlap occurred when habitat use became more similar in the presence of squawfish. For example, overlap in depth increased for juvenile suckers and juvenile trout because both shifted into riffle/run in the presence of squawfish. Species which primarily changed microhabitat use within habitats in the presence of squawfish, such as juvenile roach and stickleback in the South Fork Eel River, exhibited the smallest differences.

Discussion

The introduction of squawfish into the Eel River was associated with some dramatic changes in partitioning of habitat and microhabitat within the resident fish assemblage. Prior to the establishment of squawfish, the resident fishes were distributed throughout the width of the stream, except for the very shallow edges (<10 cm). After squawfish became established, the fishes used the deeper parts of the stream much less often, either exhibiting microhabitat shifts within habitats or changes in the use of habitats. These changes in habitat and microhabitat use resulted in decreases in spatial overlaps between many species, particularly between species which specialized in using different habitat types in the presence of squawfish.

Previous studies have also demonstrated effects of predatory fish on the spatial structure of stream fish assemblages. Schlosser (1987) and Power (1984) documented major habitat shifts (pool to riffle) in response to predation. Power et al. (1985) demonstrated both within-pool changes in depth selection and between-pool movements. Our study showed that a mixture of responses are possible, with particular species exhibiting habitat shifts, microhabitat shifts within habitats, or a combination of both.

There were some differences in the response of fishes to squawfish between the two study areas that may have reflected differences in habitat structure and recentness of invasion. At the South Fork Eel River site, juvenile rainbow trout and suckers were completely absent from pools where squawfish were present, but in the Van Duzen River, they were found in reduced numbers in shallow areas. The pools in the Van Duzen River were much more heterogeneous, with boulder cover present in some shallow areas. Also, the deepwater areas used by adult squawfish consisted of isolated pockets around boulder and bedrock outcrops; thus, large areas of the pools were probably

TABLE 6. Overlap values (Schoener 1970) for total depth, mean water column velocity, and distance to edge for threespine stickleback (STBK), California roach juveniles (RCHJ) and adults (RCHA), rainbow trout juveniles (RTJ) and adults (RTA), and Sacramento sucker juveniles (SKRJ). Overlap values from the area or time where squawfish appear are indicated by P; values in the absence of squawfish are indicated by A. The difference between overlap values is indicated by D. High values (≥0.67) are underlined.

Species pair	Total depth			Mean velocity			Edge		
	P	A	D	P	A	D	P	A	D
South Fork Eel River									
STBK–RCHJ	0.79	0.85	−0.07	0.97	0.96	0.01	0.82	0.85	−0.03
STBK–RCHA	0.72	0.72	0.00	0.70	0.80	−0.10	0.77	0.70	0.07
STBK–RTJ	0.62	0.81	−0.19	0.23	0.70	−0.47	0.74	0.75	−0.01
STBK–SKRJ	0.55	0.60	−0.05	0.09	0.85	−0.76	0.41	0.79	−0.38
RCHJ–RCHA	0.81	0.65	0.16	0.73	0.83	−0.10	0.74	0.80	−0.06
RCHJ–RTJ	0.45	0.74	−0.29	0.26	0.73	−0.47	0.51	0.81	−0.30
RCHJ–SKRJ	0.44	0.51	−0.07	0.12	0.81	−0.69	0.40	0.81	−0.41
RCHA–RTJ	0.46	0.56	−0.10	0.45	0.81	−0.36	0.62	0.79	−0.17
RCHA–SKRJ	0.46	0.71	−0.24	0.26	0.65	−0.39	0.44	0.64	−0.20
RTJ–SKRJ	0.56	0.49	0.07	0.44	0.58	−0.13	0.56	0.64	−0.08
Van Duzen River									
RCHA–RCHJ	0.71	0.76	−0.05	0.75	0.78	−0.03	—	—	—
RCHA–RTA	0.64	0.75	−0.11	0.82	0.84	−0.02	—	—	—
RCHA–RTJ	0.66	0.74	−0.08	0.72	0.87	−0.15	—	—	—
RCHA–SKRJ	0.64	0.67	−0.03	0.80	0.85	−0.05	—	—	—
RCHJ–RTA	0.66	0.69	−0.03	0.88	0.71	0.17	—	—	—
RCHJ–RTJ	0.70	0.85	−0.15	0.49	0.77	−0.28	—	—	—
RCHJ–SKRJ	0.76	0.60	0.16	0.95	0.90	0.05	—	—	—
RTA–RTJ	0.44	0.64	−0.20	0.60	0.90	−0.30	—	—	—
RTA–SKRJ	0.46	0.56	−0.10	0.93	0.80	0.13	—	—	—
RTJ–SKRJ	0.83	0.60	0.23	0.53	0.82	−0.29	—	—	—

not easily accessible to squawfish, providing refuge for the smaller fishes. In the South Fork Eel River, adult roach used pool and riffle habitat more often in the presence of squawfish but no change was noted in the Van Duzen River. The runs in the South Fork Eel River offered little cover but cover in the form of boulders and cobbles was available in runs of the Van Duzen River. Thus, the habitat shift into pools, where logs, boulders, and overhanging vegetation were available, and riffles, where shallow water and surface turbulence were available, in the South Fork Eel River may have represented a choice of habitat with cover over habitat with little cover. In the Van Duzen River, cover was available in all habitat types. In addition, the Van Duzen River study was conducted during the first summer squawfish were present at the site, but the South Fork site was occupied a minimum of 1 yr before the study. Thus, more substantial differences may still develop in the Van Duzen River.

The most extreme differences in habitat or microhabitat use occurred in sticklebacks, juvenile suckers, and juvenile rainbow trout. In the presence of squawfish, we found juvenile rainbow trout restricted almost exclusively to riffles, the only habitat type not used extensively by adult squawfish. In the Van Duzen River, large squawfish used depths >50 cm, which corresponds closely to the deepest water used by juvenile suckers (60 cm). In the South Fork Eel River, adult squawfish used depths >70 cm, and 84% of the sticklebacks observed were at depths shallower than this. These species may be especially vulnerable to predation in the Eel River because they have not experienced squawfish, or any other freshwater piscivorous fish, in their recent evolutionary history. Other studies support this hypothesis. Smith (1982) observed that threespine sticklebacks and squawfish were not found together in pools in the absence of heavy cover and suggested that the sticklebacks were eliminated from open pools by squawfish predation. Schlosser (1987) found that juvenile white suckers (*Catostomus commersoni*), which are extremely similar to Sacramento suckers in behavior and morphology, were the most susceptible fish to predation by smallmouth bass (*Micropterus dolomieui*) of the species he tested (white sucker, hornyhead chub (*Nocomis biguttatus*), and juvenile smallmouth bass). Juvenile salmonids can be a common prey of northern squawfish (*Ptychocheilus oregonensis*) in lakes and reservoirs at times (Ricker 1933, 1941; Foerster and Ricker 1941; Foerster 1968; Hartman and Burgner 1972; Eggers et al. 1978; Poe et al. 1988; Vigg et al. 1988), suggesting that salmonids may be particularly vulnerable to squawfish predation in stillwater areas.

California roach, an introduced species, exhibited the least dramatic microhabitat changes in response to the presence of squawfish. Because roach and squawfish evolved together in the Sacramento – San Joaquin drainage (Moyle 1976), the distribution of roach before the introduction of squawfish probably reflected patterns of habitat selection that evolved in response to predation by squawfish. In this situation, large shifts would not be expected. A high percentage of juvenile roach observed in pools occurred at depths utilized by adult squawfish (42% in the South Fork Eel River and 38% in the Van Duzen River),

perhaps indicating that roach have evolved effective predator avoidance behaviors for individual encounters which allow them to exploit greater depths even when squawfish are present.

The effects of squawfish on rainbow trout are potentially important from a management perspective because of the significance of the sport fishery for steelhead (anadromous rainbow trout) in the Eel River. We feel that the changes we have documented are relatively unimportant from this perspective because trout and squawfish tend to be spatially segregated on the basis of differences in the physical environment, particularly temperature (Moyle and Nichols 1973; Dettman 1976; Moyle and Daniels 1982; Smith 1982; Baltz et al. 1987). Rainbow trout are most abundant in cool headwater and tributary streams. Squawfish are most abundant in the warmer downstream portions of streams and in warm tributaries. This pattern is also found in the Eel River system (L. R. Brown and P. B. Moyle, unpubl. data). Squawfish are most abundant in downstream areas or tributaries that are too warm to provide good trout habitat, although there are a few exceptions such as the Van Duzen River (L. R. Brown and P. B. Moyle, unpubl. data). Thus, the presence of squawfish does not affect the majority of the oversummering salmonid population. Production in the limited areas of overlap may be reduced due to direct predation, increased mortality due to heat stress because thermal refugia (thermal stratification and spring inflow) occurring in pools are no longer available, and decreased growth due to crowding in the limited riffle areas available. Predation during outmigration of smolts may be important but evidence from other systems suggests that outmigration losses are relatively small in natural streams (Brown and Moyle 1981).

Squawfish are a common species in California streams (Moyle 1976). Previous work has suggested that squawfish are an important influence on spatial partitioning within California stream fish assemblages (Moyle and Baltz 1985). Our data verify the importance of squawfish as a driving force in determining spatial partitioning. Further work is needed to determine if squawfish can cause changes in size distributions, relative abundances, and densities of resident fishes. If our results for Sacramento squawfish can be applied to the other members of the genus, which are common in Pacific Coast drainages, squawfish predation may be found to be of widespread importance in determining the spatial structure of many stream fish communities.

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Interactions between Two Distantly Related Species, Brook Trout[1] (*Salvelinus fontinalis*) and White Sucker (*Catostomus commersoni*)

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We compared spatial distribution and food habits of an allopatric brook trout (*Salvelinus fontinalis*) population to one living sympatrically with white sucker (*Catostomus commersoni*) in two small oligotrophic lakes. Small brook trout (<20 cm) of both sympatric and allopatric populations were more abundant in the littoral than in the offshore zone whereas large (≥20 cm) were found equally in both habitats in May. From June to August, small and large trout from both populations shifted to the offshore zone; this shift was more pronounced for small sympatric trout. Allopatric trout fed mainly on zoobenthos whereas sympatric trout fed mainly on zooplankton except small ones which ate mostly zoobenthos during May and June. White sucker (<20 and ≥20 cm) were generally found in the littoral zone, feeding mainly on zoobenthos. These results suggest that brook trout shifted their spatial distribution and/or their feeding habits in the presence of white sucker and that the nature of these interactions varied according to fish size. Diet overlap between trout and sucker was the lowest when the biomass of benthic prey in the littoral zone was lowest (July), indicating that the intensity of interaction among these species varies according to the abundance of food resources.

Nous avons comparé la distribution spatiale et l'alimentation d'une population allopatrique d'omble de fontaine (*Salvelinus fontinalis*) et d'une autre vivant en sympatrie avec du meunier noir (*Catostomus commersoni*) dans deux petits lacs oligotrophes. Les petits ombles de fontaine (< 20 cm) sympatriques et allopatriques étaient plus abondants en zone littorale qu'en zone pélagique alors que les grands (≥ 20 cm) étaient également retrouvés dans les deux habitats, en mai. De juin à août, les petits et les grands ombles des deux populations ont effectué un déplacement vers la zone pélagique. Ce déplacement a cependant été plus prononcé chez les petits ombles sympatriques. Les ombles allopatriques s'alimentaient principalement de zoobenthos alors que les ombles sympatriques s'alimentaient principalement de zooplancton, à l'exception des petits ombles sympatriques qui ont consommé principalement du zoobenthos en mai et juin. Les meuniers noirs (< 20 et ≥ 20 cm) étaient généralement retrouvés en zone littorale, s'alimentant principalement de zoobenthos. Ces résultats suggèrent que les ombles de fontaine ont déplacé leur distribution spatiale et/ou leur alimentation en présence du meunier noir et que la nature des interactions entre ces espèces varie en fonction de la taille des individus. Le recouvrement alimentaire entre les ombles et les meuniers était le plus faible lorsque la biomasse des proies benthiques était à son plus faible dans la zone littorale (juillet), suggérant que l'intensité des interactions entre ces espèces varie en fonction de l'abondance des ressources alimentaires.

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Because traditionally most theories of interspecific competition assumed equilibrium in environmental conditions (e.g. MacArthur and Levins 1967; MacArthur 1972; Turelli 1981), competition has been considered by many to be relatively constant through time. In the real world the environment often fluctuates, and competition, as a strong selective force, may be intermittent, occurring only during lean periods (Schoener 1982). In addition, interactions between distantly related species have received little attention (Diamond 1978; Schluter 1986; Persson 1987a). It is generally assumed that interactions are more intense between closely related species because of their high potential of niche overlap. In fact, distantly related species may interact between themselves as intensely, in terms of niche shift, character displacement (sensu Schluter 1986), and impact on growth or on production of populations (O'Neill and Hyatt 1986; Persson 1987a; Magnan 1988). It should be pointed out that distantly related species often use quite different strategies to exploit a common resource, increasing the possibility of asymmetrical competition (sensu Connell 1983). Finally, extensive ontogenetic shifts in diet and in habitat use are nearly universal in fish, partly because resource exploitation abilities vary with body size (Werner and Gilliam 1984). One implication of these ontogenetic niche shifts in species interactions is that competition may occur only among specific life history stages, and then involve competitive bottlenecks (Werner 1986; Persson 1987b).

The white sucker (*Catostomus commersoni*) was introduced by bait fishermen in many brook trout (*Salvelinus fontinalis*) lakes of Quebec (Canada) 30–50 yr ago and may naturally overlap in distribution with trout (Scott and Crossman 1973). In a survey of 18 oligotrophic Quebec lakes, Magnan (1988) found that (1) the mean annual yield (kilograms per hectares) of trout was significantly reduced when they lived sympatrically with white sucker and (2) trout shifted their food habitats from

[1]The authors prefer the common name "charr" to designate species of the genus *Salvelinus*.

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benthic organisms to zooplankton in the presence of sucker. Although these results indicate that interspecific competition is important in these systems, they give no information on the mechanisms involved in these interactions.

To investigate the mechanisms involved in the niche shift of brook trout, we compared spatial distribution and food habits (prey type and size) of an allopatric brook trout population with one living sympatrically with white sucker. Comparisons were also made when both species lived in sympatry. There are no lakes in the area which contain only white sucker. Because benthic organisms appeared to be the preferred prey of both trout and sucker (Magnan and FitzGerald 1982; Magnan 1988; Lachance and Magnan 1990), we sampled the littoral zoobenthos to examine (1) if the benthic fauna was comparable among lakes (qualitatively and quantitatively), (2) how each species used this resource, and (3) the effect of fluctuation of a common preferred resource on species interactions. Comparisons were made on two size classes of both trout and sucker to determine whether resource utilization and species interactions varied according to size.

Study Lakes

We studied Lake Vautour with an allopatric brook trout population and Lake Sauterelle with a sympatric brook trout and white sucker population from lakes surveyed by Magnan (1988). Both lakes are in the Mastigouche Reserve, Quebec, Canada (46°38′N, 73°15′W) and are small (7.3 and 7.5 ha), shallow (maximum depth 16.8 and 13.7 m; mean depth 4.8 and 5.3 m), and low in conductivity (12.5 and 11.2 $\mu S \cdot cm^{-1}$). Between May and August 1985, the lakes were thermally stratified, the transparency (Secchi disk) ranged from 3.6 to 4.5 m, and dissolved oxygen ranged from 10.4 to 12.6 ppm in the epilimnion. The two lakes were 66 km apart, are subject to sportfishing (brook trout), and exploitation is carefully controlled by the Quebec government (see Magnan 1988).

Apart from brook trout, Lake Vautour contained northern redbelly dace (*Phoxinus eos*). Brook trout, white sucker, northern redbelly dace, and pearl dace (*Semotilus margarita*) were found in Lake Sauterelle. The northern redbelly dace and pearl dace were not taken into account for this study.The northern redbelly dace has no significant effect on the yield of brook trout (Magnan 1988). Also, gillnet fishing carried out in Lake Sauterelle indicated that the relative biomass of pearl dace represented less than 1% of the total biomass of the fish captured (Magnan 1988).

Materials and Methods

Fish Sampling

We studied the spatial distribution of the fish from captures in the littoral (0–2 m depth) and offshore (0–4 m depth) zones during May 24–28, June 18–20, July 11–13, and August 7–10, 1985. Fish were captured with experimental multifilament gill nets (1.8 m deep × 38.1 m long, with stretched mesh of 2.5, 3.8, 5.1, 6.4, and 7.6 cm). In the littoral zone, nets were arbitrarily set parallel to the shore in 1.5–2.0 m of water whereas in the offshore zone, two nets were superimposed, giving an effective fishing gear of 3.6 × 38.1 m. Additional nets of 1.5 m deep × 30.0 m long (stretched mesh of 2.5 cm) were used in the littoral zone. The number of nets used in both zones varied among lakes and sampling dates according to the sample size needed for the feeding habits study (see below). Nets were set between 20:00 and 24:00 and between 02:00 and 06:00 because species studied are presumably more active during these periods (Reynolds and Casterlin 1978; Power 1980). We noted the time and the place of capture, the position of the fish in the water column (±5 cm), and their total length. Size frequency distribution of both trout and sucker showed distinct modes that allowed the separation of fish into two size classes for subsequent analyses: <20 cm (12–19.9 cm) and ≥20 cm (20–35 cm), referred to hereafter as small and large fish, respectively. These size classes should correspond to age 1+ and ≥2+ trout and sucker (Scott and Crossman 1973; Magnan and FitzGerald 1982, 1983).

Stomach Content Analysis

A mean of 20 fish per size class, per species, per sampling date, and per lake were used in the analysis of feeding habits (excluding empty stomachs). Because we cannot assume that fish captured in littoral or offshore zones obtained their food there, we considered stomach contents from fish according to the percent of captures in each zone. Stomachs were placed in 10% formaldehyde following fish removal from the nets. For the brook trout, the content of the digestive tract between the oesophagus and the pyloric valve was examined (Magnan and Fitzgerald 1982). There is no distinct separation between the stomach and intestine of the white sucker; therefore, we examined the first third of the digestive tract (cf. Ringler and Johnson 1982). All prey were generally identified to family and measured to the nearest 0.01 mm (total length, without antennae and appendages, and width of the cephalic capsule) using an ocular micrometer mounted on a dissecting scope (40×). We only subsampled Cladocera and Copepoda when there were more than 60 in a stomach. The weight of each organism ingested was estimated using simple linear regressions (total length – dry weight). Regressions for benthic organisms were computed from our data (see zoobenthos sampling), that of prey fish with 130 northern redbelly dace (the only fish species found in stomachs), and that of terrestrial insects from specimens found in stomachs (P. Magnan, unpubl. data). For Cladocera and Copepoda, we used published regression equations for *Daphnia g. mendotae* and *Cyclops vernalis* (nonovigerous females) (Culver et al. 1985). Finally, we computed a general length – dry weight regression with data extending from copepods to ephemeropterans to estimate weight of the less abundant taxa and of those for which we found no significant relationships ($r = 0.94$, $p < 0.0001$; P. Magnan, unpubl. data). The weight of only 4.5% of the 75 217 prey found in stomachs was estimated using this general equation. The estimations of prey weight allowed us to compare the diet of each population using the mean percent weight of prey method (Hyslop 1980), which overcomes the criticism of percent occurrence and percent number methods (Wallace 1981).

We computed diet overlap between sympatric brook trout and white sucker for each sampling session with the niche overlap index of Schoener (1970). This index, which ranges from 0 (no overlap) to 1 (complete overlap), is the most appropriate for overlap estimates ranging between 0.07 and 0.85 (Linton et al. 1981; Wallace 1981).

Zoobenthos Sampling

In May 1985, we identified the microhabitats in the littoral zone of each lake by scuba diving (cf. Laughlin and Werner

1980; Mittelbach 1981; Eadie and Keast 1981). Two distinct microhabitats were found in the littoral zone at Lake Vautour, one of sand substrate covered with scattered stems of *Sparganium* spp. and the other of decomposed organic matter. Lake Sauterelle had a single substrate characterized by a mixture of sand and decomposing organic matter. Three stations were arbitrarily sampled in each microhabitat. Three samples were taken at each station between 08:00 and 18:00 using a standard Ekman dredge (231 cm^2), yielding 18 and 9 samples for each sampling period in Lakes Vautour and Sauterelle, respectively. An exception existed for Lake Vautour (May) where logistical problems allowed us to take only 10 Ekman dredge samples. Similar sample sizes have been used to quantitatively describe littoral zoobenthos (i.e. <2 m depth) in comparable lakes (Post and Cucin 1984; Dermott 1988; Hanson et al. 1989). In the field, the samples were sieved through a No. 30 US sieve and placed in a 10% formaldehyde solution. In the laboratory, organisms were generally identified to family and counted. A subsample of 50 organisms from each taxon was taken to determine length–weight relationships. Each organism was measured (total length and width of the cephalic capsule) to the nearest 0.01 mm and weighed to the nearest 0.01 mg, after drying 24 h at 80°C. These data permitted estimation of the length–weight relationships.

Data Analyses

Spatial distribution of fish was analysed using a *G*-test (Sokal and Rohlf 1981). Specifically, we tested two null hypotheses: (1) there were no significant differences in the spatial distribution of the fish between the littoral and offshore zones and (2) there were no significant differences in the vertical distribution of the fish between the upper and lower parts of the water column. We considered the lower part of the water column to be between 1.5 and 2.0 m depth in the littoral zone and between 3.0 and 4.0 m depth in the offshore zone. The upper part of the water column was from 1.5 m depth to the surface in the littoral zone and from 3.0 m depth to the surface in the offshore zone. As the number of gill nets varied among lakes and sampling dates, the expected frequencies for the *G*-test were determined on the basis of fishing effort (i.e. littoral versus offshore zone and upper versus lower part of the water column; e.g. Hume and Northcote 1985). In this way, if we had two gillnet set in the littoral zone and one in the offshore zone, the expected ratio was 2:1 for the testing of hypothesis. 1. The expected frequencies were always 3:1 for hypothesis 2, since fishing effort was three times higher in the upper part than in the lower part of the water column. No *G*-test was performed when the sample size was lower than six.

A Kolmogorov–Smirnov test was used to determine (1) if the weight frequency distribution of the benthic organsims found in the resource varied among lakes and (2) if the weight frequency distribution of benthic prey eaten by trout sucker differed from that in the lake. A Mann–Whitney *U*-test was used to compare the monthly abundance of each taxon between the two lakes. We used a *t*-test on log (x) transformed data to determine if the mean density and relative biomass (grams per square metre) of benthic organisms differed between the two lakes on each sampling date.

To investigate the effect of fluctuation of a common preferred resource on species interactions, we compared the diet overlap between sympatric brook trout and white sucker with the abundance of benthic resources of the littoral zone at the different sampling periods (e.g. Lammens et al. 1985; DuBowy 1988). Comparisons of diet overlaps were also made between sympatric and allopatric trout populations.

Results

Horizontal Distribution

In May, small brook trout of sympatric and allopatric populations were significantly more abundant in the littoral than in the offshore zone ($p < 0.05$) whereas large brook trout were found equally in both habitats ($p > 0.05$; Fig. 1 and 2). From June to August, trout from both populations exhibited a shift to the offshore zone ($p < 0.05$; Fig. 1 and 2); two exceptions to this pattern were small sympatric and small allopatric brook trout in June and July, respectively, that were captured equally in the littoral and offshore zones ($p > 0.05$). It is noteworthy that in July and August, the shift to the offshore zone was more pronounced for small sympatric than for small allopatric brook trout (Fig. 1). Catches in the 2.5-cm stretched mesh nets confirmed this trend, as small allopatric trout were present in the littoral zone from May to August whereas small sympatric ones were scarce in this zone in May and June and absent in July and August (Fig. 3).

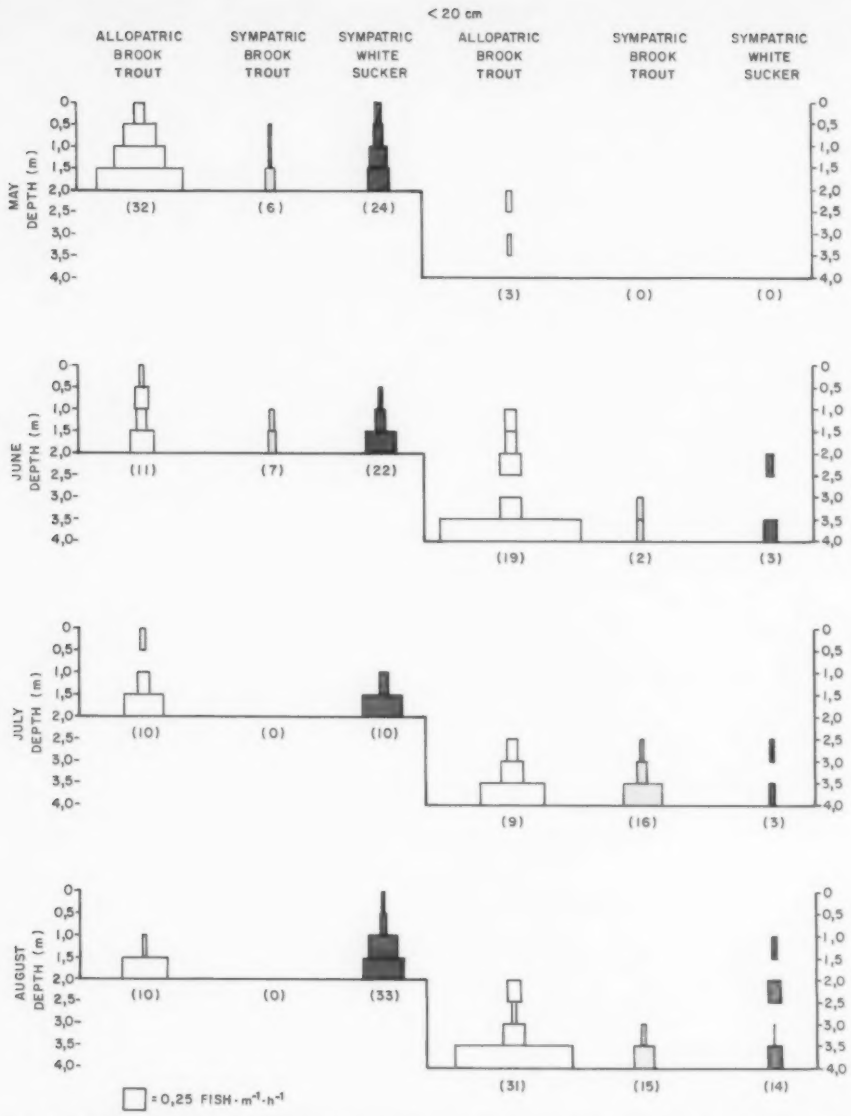
Sympatric white sucker were generally more abundant in the littoral than in the offshore zone ($p < 0.05$; Fig. 1 and 2). Exceptions to this pattern were small individuals (in June) and large ones (in June and July) that showed no significant differences in their spatial distribution among the two zones and large individuals (in August) that were significantly more abundant in the offshore zone ($p < 0.05$; Fig. 1 and 2).

Vertical Distribution

Brook trout (sympatric and allopatric) as well as white sucker were significantly more abundant in the lower than in the upper part of the water column in both littoral and offshore zones ($p < 0.05$; Fig. 1 and 2). Eleven of the 38 cases tested made exception to this general pattern: for small individuals, white sucker (littoral zone in May) and brook trout (sympatric and allopatric, littoral zone in June); for large individuals, allopatric brook trout (littoral zone from May to August and offshore zone in May), sympatric brook trout (offshore zone in May), and white sucker (offshore zone in May and August). In these cases, there was no significant difference in spatial distribution in the lower and upper parts of the water column.

Feeding Habits

In May and June, small sympatric and allopatric brook trout had a similar diet. Individuals of both populations fed mainly on zoobenthos (i.e. >50% in weight) and little on zooplankton (Table 1). Small allopatric trout also fed up to 15% (in weight) on terrestrial insects in May (Table 1). In July and August, small allopatric trout fed mainly on zoobenthos and on fish or terrestrial insects whereas small sympatric trout shifted their diet to zooplankton (i.e. >50% in weight; Table 1). From May to August, the main benthic organisms found in the stomach contents of small trout were, by decreasing order, Ephemeroptera, Odonata, Trichoptera, and Sialidae larvae and Corixidae (Table 1). Zooplankton was mainly composed of Chaoboridae throughout the summer, except in August when Cladocera were also important (Table 1). Ingested Cladocera were almost exclusively *Daphnia* spp. and *Holopedium gibberum* (S. Tremblay and P. Magnan, pers. obs.).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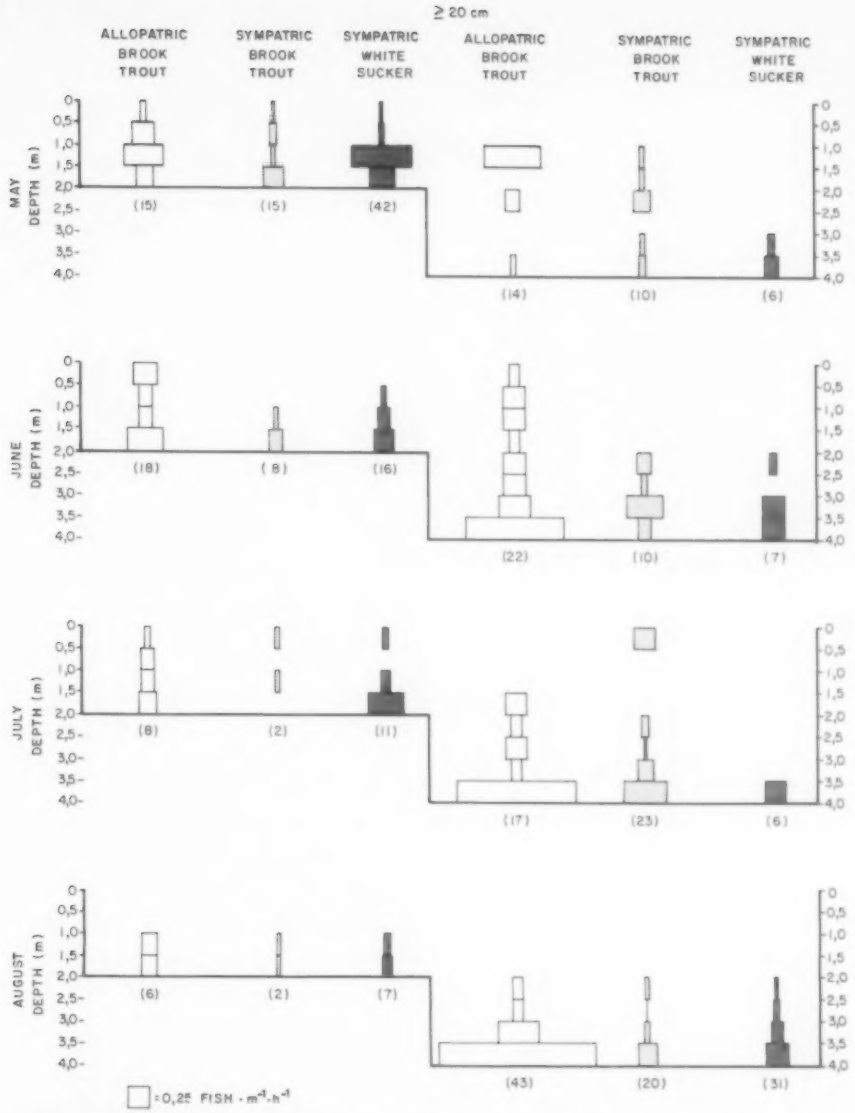
MAY DEPTH (m)
(32) (6) (24) (3) (0) (0)
JUNE DEPTH (m)
(11) (7) (22) (19) (2) (3)
JULY DEPTH (m)
(10) (0) (10) (9) (16) (3)
AUGUST DEPTH (m)
(10) (0) (33) (31) (15) (14)
= 0,25 FISH · m⁻¹ · h⁻¹

FIG. 1. Spatial distribution of small fish (<20 cm) in the littoral (2-m contour) and offshore (4-m contour) zones in Lakes Vautour (allopatric population) and Sauterelle (sympatric populations), as estimated with experimental gill nets from May to August 1985. The number of fish captured is indicated in parentheses.

From May to July, small sympatric white sucker fed mainly on benthic organisms and little on zooplankton whereas in August their diet was equally composed of zoobenthos and zooplankton (Table 1). Diptera (Chironomidae), Ephemeroptera, and Trichoptera larvae were the dominant benthic prey found in their stomachs whereas Cladocera (*Daphnia* spp., *H. gibberum*, and *Bosmina* spp.) and, to a lesser extent, Chaoboridae and Diptera pupae were the main zooplankters (Table 1).

The diet of large sympatric and allopatric brook trout differed through the summer 1985. Although individuals of both populations fed mainly on zoobenthos in May (i.e. >50% in weight), sympatric trout consumed up to 4 times more plankton than allopatric ones (Table 1). From June to August, large allopatric trout fed mostly on zoobenthos, and also on fish in July, whereas large sympatric trout ate mainly zooplankton (Table 1). The benthic prey consisted mainly of Ephemeroptera, Odonata, Trichoptera, and Sialidae larvae whereas zooplankton was mainly composed of Chaoboridae, except in August when Cladocera (*Daphnia* spp. and *H. gibberum*) were also important (Table 1).

Large white sucker consumed principally benthic organisms during the four sampling periods (Table 1). Diptera (Chironomidae), Ephemeroptera, Odonata, and Trichoptera larvae, Gammaridae, and annelids were the most important components among benthic prey found in their diet through the summer, whereas Chaoboridae were the principal zooplankters from May to July (Table 1). In August, the zooplankton eaten was


≥ 20 cm
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SYMPATRIC WHITE SUCKER
MAY DEPTH (m)
(15) (15) (42) (14) (10) (6)
JUNE DEPTH (m)
(18) (8) (16) (22) (10) (7)
JULY DEPTH (m)
(8) (2) (11) (17) (23) (6)
AUGUST DEPTH (m)
(6) (2) (7) (43) (20) (31)
0 0,5 1,0 1,5 2,0 2,5 3,0 3,5 4,0
= 0,25 FISH · m⁻² · h⁻¹

FIG. 2. Spatial distribution of large fish (≥20 cm) in the littoral (2-m contour) and offshore (4-m contour) zones in Lakes Vautour (allopatric population) and Sauterelle (sympatric populations), as estimated with experimental gill nets from May to August 1985. The number of fish captured is indicated in parentheses.

mainly composed of Cladocera (*Daphnia* sp., *H. gibberum*, and *Bosmina* sp.) (Table 1).

Apart from the differences between trout and sucker presented above, there is a noteworthy similarity. Results showed an increasing proportion of zooplankton in the fish diet from May to August that was more pronounced for small sympatric trout and sucker and for large sympatric trout (Table 1).

For each comparison, the Schoener (1970) index showed that the minimum overlap between populations was always in July (Table 2). The weight frequency distribution of benthic prey ingested by both sympatric and allopatric brook trout (small and large fish) and by large white sucker was significantly different from that found in the resource (Kolmogorov–Smirnov test, $p < 0.001$; Table 3). In contrast, small white sucker consumed benthic prey according to a size pattern similar to that found in the resource with the exception of May, where a significant difference was observed (Kolmogorov–Smirnov test, $p < 0.001$; Table 3).

Benthic Resource of the Littoral Zone

The abundance of main benthic taxa did not differ significantly between the two lakes from May to August, with the exception of the Gammaridae, Chironomidae larvae, and Diptera pupae in May and the Gammaridae in July (Mann–Whitney *U*-test, $p < 0.05$; Table 4). The mean density of benthic orga-

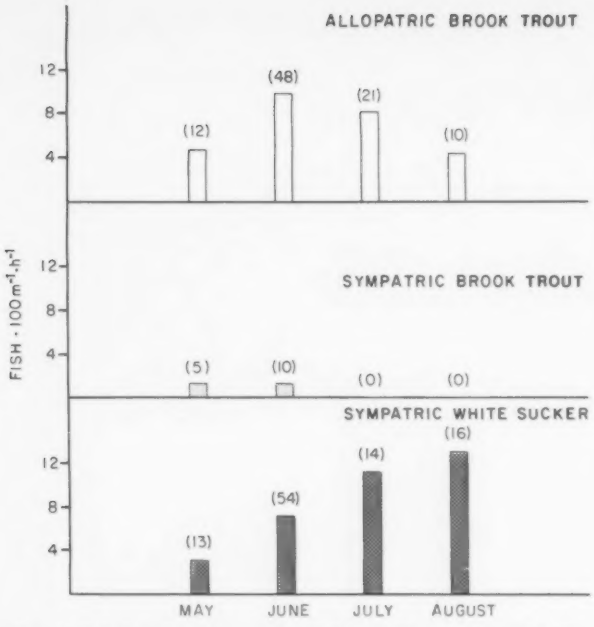

FIG. 3. Relative abundance of small fish (<20 cm) captured in the littoral zone (2-m contour) of Lakes Vautour (allopatric populations) and Sauterelle (sympatric populations), as estimated with gill nets (stretched mesh nets of 2.5 cm) from May to August 1985. The number of fish captured is indicated in parentheses.

nisms (total) was significantly higher in Lake Vautour than in Lake Sauterelle in May whereas their mean relative biomass (grams per square metre) was significantly higher in Lake Vautour than in Lake Sauterelle in May and July (t-test, $p < 0.05$; Table 4). The weight frequency distribution of benthic organisms found in the littoral zone of Lakes Vautour and Sauterelle was significantly different on the four sampling dates (Kolmogorov–Smirnov test, $p < 0.01$)

Discussion

The results of this study indicate that brook trout shifted their spatial distribution and/or their feeding habits in the presence of white sucker and that these interactions vary according to the size of the fish. The similarity in spatial distribution and habitat shift between sympatric and allopatric brook trout populations is striking and may be driven by changes in both food supply in the littoral zone (Table 4) and thermal regime (Table 5; e.g. Persson 1987a), regardless of whether the white sucker are present or not. However, the apparent evacuation of the littoral zone by small sympatric trout in contrast with partial abandonment by small allopatric ones in late summer could be due to either direct or indirect effects of sucker on trout. Catch and diet data coincide, as small allopatric brook trout fed mainly on zoobenthos throughout the summer whereas small sympatric ones shifted their diet from zoobenthos in May and June to zooplankton in July and August. Unlike small sympatric trout, large sympatric trout ate more zooplankton than allopatric trout throughout the summer. Niche shift is among the strongest evidence that interspecific competition occurs in natural communities (Diamond 1978; Werner 1986). Therefore, our results indicate competitive interaction between different size classes of brook trout and white sucker. Large sympatric trout shifted their spatial distribution and diet sooner than small ones, presumably because of metabolic constraints related to their size. Persson (1987b) found that 1+ perch (*Perca fluviatilis*) had both a higher growth rate and a greater ability to withstand resource depression than 2+ perch, based on the lower metabolic demand of 1+ perch.

Alternatively, the observed differences in spatial distribution and/or feeding habits between sympatric and allopatric brook trout might result from differences in both habitat and food resources between the two lakes. Scuba diving indicated the presence of two microhabitats in the littoral zone of Lake Vautour compared with only one in Lake Sauterelle. Also, benthos sampling indicated that density and relative biomass of benthic organisms were higher in Lake Vautour. Stomach content analysis indicated that terrestrial insects were found almost only in the diet of trout from Lake Vautour. Although these apparent differences in food resource might be due to direct or indirect effect of white sucker, they might be simply due to differences between the two lakes.

Indirect evidence indicates that the diet shift of sympatric brook trout results from interactions with white sucker. First, comparisons of diet from seven allopatric and five sympatric brook trout populations of the same area confirmed that trout shifted their diet from zoobenthos to zooplankton in the presence of white sucker (Magnan 1988). Second, we observed that diet overlap between trout and sucker was the lowest when the relative biomass (grams per square metre) of benthic organisms was also the lowest in Lake Sauterelle in July. Specifically, lower diet overlap corresponded to the lowest relative biomass (mean density × mean weight; Table 4) of both Ephemeroptera and Odonata (combined), which were among the preferred prey of trout and sucker throughout the summer. This result indicates that the intensity of interactions between brook trout and white sucker varies according to the abundance of food resources and agrees with Schoener's (1982) hypothesis. Schoener (1982) stated that during times of plenty, the species would converge upon the same resource types because they are abundant and then become more profitable than resource types for which trophic phenotypes have been selected for; during lean times, each species would segregate upon resource types for which they are best adapted. Lammens et al. (1985), Schmitt and Holbrook (1986), and Prejs and Prejs (1987) with fish and DuBowy (1988) with dabbling ducks also observed that feeding overlap among species was lowest when food resources were also the lowest, suggesting that mechanisms underlying such niche shift and resource partitioning are a reduction of food levels. Diamond (1978) stressed the importance of measuring resource levels in studies of species interactions to make this essential link between niche shift and interspecific competition.

Generally, coexisting species partition the food resources according to their functional morphology and their ability to exploit a given type of prey (Gatz 1979; Laughlin and Werner 1980; Magnan and FitzGerald 1984; Lammens et al. 1985). White sucker is better adapted than brook trout to feed on zoobenthos whereas brook trout is better adapted to feed on zooplankton. Generally, fish having an inferior mouth are more effective bottom feeders whereas fish with a terminal mouth are more effective in capturing surface–water and midwater prey (Alexander 1967; Schutz and Northcote 1972; Gatz 1979; Magnan and FitzGerald 1984). Furthermore, our results indicate that the two species have very different feeding behaviors. Allopatric as well as sympatric brook trout fed on the largest benthic prey available whereas white sucker consumed benthic

TABLE 1. Mean percent weight of prey found in the stomach contents of fish captured in Lakes Vautour (allopatric population) and Sauterelle (sympatric populations) from May to August 1985.

Prey type	Fish <20 cm			Fish ≥20 cm		
	Allopatric brook trout	Sympatric brook trout	Sympatric white sucker	Allopatric brook trout	Sympatric brook trout	Sympatric white sucker
			May 1985			
Zooplankton						
Cladocera			0.7			*T*[a]
Copepoda			1.7		*T*[a]	0.1
Chaoboridae	6.5	6.8		8.2	38.3	12.8
Diptera (pupae)			5.8		0.1	1.1
Total	6.5	6.8	8.1	8.2	38.5	13.9
Zoobenthos						
Gammaridae	0.2	1.1		0.1	*T*[a]	
Diptera	0.4	0.2	59.2	*T*[a]	0.3	24.3
Trichoptera	6.9	1.9	7.3	1.4	0.8	7.9
Corixidae	0.2	2.0	0.5	1.1	3.0	0.6
Sialidae	31.1	1.3		12.8	0.9	
Ephemeroptera	43.9	66.7	16.8	31.2	35.3	32.7
Odonata	9.2	14.1	3.1	17.8	6.0	8.3
Annelids			4.6		1.4	10.9
Others	*T*[a]	4.1		5.7	7.4	*T*[a]
Total	91.9	91.3	91.5	70.2	55.2	84.7
Fish		0.1		5.8	1.5	
Other aquatic organisms	0.6	1.1	*T*[a]	7.6	4.8	*T*[a]
Terrestrial insects	1.1	0.7	0.3	8.2		1.4
N[b]	20	12	22	23	23	26
n[c]	1.3	0.5	0.3	3.3	3.2	1.5
			June 1985			
Zooplankton						
Cladocera	0.1	2.3	24.8			1.2
Copepoda			0.2			0.1
Chaoboridae	18.5	21.5	1.6	16.5	48.5	14.3
Diptera (pupae)		0.1	2.3	0.2		1.3
Total	18.6	23.9	28.9	16.7	48.5	16.9
Zoobenthos						
Gammaridae	0.1	0.4	0.4	2.0		
Diptera	4.2	0.1	40.4	0.1	0.1	29.9
Trichoptera	1.6	1.7	11.7	0.6	0.4	15.3
Corixidae	0.1	0.6	*T*[a]	0.1	0.6	0.2
Sialidae	1.0	0.4	0.1	0.9	0.1	2.1
Ephemeroptera	30.1	43.5	15.1	56.7	23.3	12.4
Odonata	21.3	25.8	2.7	7.4	18.7	17.8
Annelids		0.3	0.4	0.1	0.2	5.3
Others	*T*[a]		*T*[a]			0.1
Total	58.3	72.6	70.9	67.9	43.5	83.1
Fish	4.7	2.6		7.9	7.0	
Other aquatic organisms	2.3	*T*[a]		1.4		
Terrestrial insects	16.1	0.8	0.2	6.1	1.0	
N[b]	20	21	21	21	18	19
n[c]	1.4	1.3	0.2	4.1	3.9	0.9

prey according to a size pattern similar to that found in the resource. Laboratory observation showed that brook trout select their prey one by one, presumably according to size, whereas white sucker obtain their food by sieving the sediment, and thus making no or little selection for prey size (P. Magnan, pers. obs.). Therefore, the feeding niche of white sucker completely overlaps with that of brook trout on the benthic prey size axis, especially during periods of low levels of benthic resource. In terms of limiting similarity (MacArthur and Levins 1967; MacArthur 1972; Roughgarden 1974; Werner 1977), such a

TABLE 1. (*continued*)

Prey type	Fish <20 cm			Fish ≥20 cm		
	Allopatric brook trout	Sympatric brook trout	Sympatric white sucker	Allopatric brook trout	Sympatric brook trout	Sympatric white sucker
			July 1985			
Zooplankton						
Cladocera	1.6	0.5	7.1	T[a]	0.6	3.4
Copepoda			0.2			T[a]
Chaoboridae	5.3	57.5	5.7	0.7	70.1	10.2
Diptera (pupae)	1.9	0.2	5.9	T[a]		2.6
Total	8.9	58.3	18.9	0.7	70.7	16.1
Zoobenthos						
Gammaridae			5.4			0.3
Diptera	0.5	0.2	55.9	T[a]	0.2	33.5
Trichoptera	10.7	0.1	6.3	5.8	1.7	3.8
Corixidae	T[a]	6.6	2.1		1.7	0.5
Sialidae	0.3	1.1	0.4		0.4	1.4
Ephemeroptera	45.1	21.6	5.5	51.4	12.6	21.2
Odonata	3.2	12.2	3.8	2.2	1.1	21.5
Annelids			0.7	2.8	T[a]	0.5
Others	T[a]		1.1			0.1
Total	59.9	41.7	81.1	62.3	17.8	82.7
Fish	27.5			35.7	11.2	
Other aquatic organisms	1.0			1.0		
Terrestrial insects	2.8	0.1		0.3	0.4	1.2
N[b]	20	17	19	20	20	21
n[c]	2.5	1.2	0.1	5.4	3.3	1.1
			August 1985			
Zooplankton						
Cladocera	9.2	21.2	47.2	19.5	12.7	16.9
Copepoda			T[a]			T[a]
Chaoboridae	14.1	43.5	1.3	5.2	49.1	2.6
Diptera (pupae)	4.9	1.3	0.5		0.6	1.9
Total	28.2	66.0	48.9	24.7	62.3	21.5
Zoobenthos						
Gammaridae			0.1			T[a]
Diptera	1.0	6.0	39.9	4.4	2.3	37.7
Trichoptera	0.6		0.4	16.8	1.5	7.4
Corixidae		3.6	0.1	0.4	0.8	0.8
Sialidae	0.6		1.4	T[a]		1.3
Ephemeroptera	21.5	11.6	6.0	35.1	17.0	10.9
Odonata	11.6	12.6	0.3	13.2	13.0	11.5
Annelids			3.0	0.5		8.8
Others	T[a]					0.2
Total	35.2	33.7	51.1	70.3	34.6	78.5
Fish					3.1	
Other aquatic organisms	1.0			4.4		T[a]
Terrestrial insects	35.6	0.2		0.7		
N[b]	21	16	19	22	21	20
n[c]	0.4	0.3	0.1	2.1	2.0	1.5

[a]Indicates values less than 0.05%.
[b]Number of stomach contents analysed.
[c]Total dry weight (g) of prey found in the stomach.

behavior of white sucker leaves few possibilities to the brook trout to take a competitive refuge on the benthic prey size axis.

The amount of energy available to fish in lake systems seems to be independent of the number of species present (Hanson and Leggett 1982). In the present study, the catch of brook trout per unit of effort were much lower in the presence of white sucker. Moreover, a study carried out on 18 lakes of the same area (Magnan 1988) indicated that the presence of white sucker

TABLE 2. Feeding overlap (Schoener (1970) index) among the different populations studied in Lakes Vautour (allopatric population) and Sauterelle (sympatric populations) from May to August 1985.

Population	May	June	July	August
		Fish <20 cm		
Sympatric brook trout vs. sympatric white sucker	0.23	0.25	0.18	0.37
Sympatric brook trout vs. sympatric white sucker (≥20 cm)	0.51	0.46	0.46	0.50
Allopatric brook trout vs. sympatric brook trout	0.65	0.76	0.32	0.49
		Fish ≥20 cm		
Sympatric brook trout vs. sympatric white sucker	0.55	0.46	0.28	0.43
Allopatric brook trout vs. sympatric brook trout	0.60	0.56	0.28	0.52

NOTE: Feeding overlap was calculated from the mean percent weight of the prey ingested.

reduces by nearly half the brook trout yield (kilograms per hectare). This effect of white sucker on brook trout is presumably related to the niche shift of trout on zooplankton, a food of inferior quality in terms of energy. Hanson and Leggett (1986) considered microcrustaceans (e.g. *Ceriodaphnia* spp., Chydoridae, and Ostracoda) to be a food source of low energetic value when compared with macroinvertebrates. Furthermore, Persson's (1987b) data indicated that a *Sialis* sp. larvae can have the same energy content as 600 *Daphnia magna*. Interspecific competition for macroinvertebrates between trout and sucker would therefore constitute a bottleneck (sensu Persson 1987b) for sympatric brook trout. This competitive bottleneck should occur among young-of-the-year brook trout because their diet and spatial distribution overlapped with those of small and large white sucker (H. Venne and P. Magnan, in prep.). In a river system, Rose (1986) observed a reduction in growth rate of brook trout during the first summer, in the presence of rainbow trout (*Oncorhynchus mykiss*, formerly *Salmo gairdneri*). He suggested that this reduction in growth may result in increased overwintering mortality of fish at high latitude and may be a mechanism by which brook trout are excluded by rainbow trout (Rose 1986). Because small and large white sucker feed to diverse degrees on zooplankton, a competitive bottleneck may also exist between the brook trout larvae and the white sucker during the zooplanktonic stage.

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TABLE 3. Mean weight (mg), 95% confidence intervals (in parentheses), and range of benthic organisms found in the littoral zone and in the stomachs of fish captured in Lakes Vautour (allopatric population) and Sauterelle (sympatric populations) from May to August 1985 (log (x) back-transformed data). In square brackets: left, number of samples or stomach contents analysed; right, number of benthic organisms.

	May	June	July	August
		Vautour Lake		
Resource	0.16 (0.15–0.17) 0.01–36.18 [10, 890]	0.15 (0.14–0.17) 0.01–53.72 [20, 750]	0.17 (0.15–0.18) 0.01–55.63 [17, 624]	0.10 (0.10–0.11) 0.01–38.12 [19, 1538]
Brook trout <20 cm	2.27 (2.13–2.14) 0.12–18.63 [20, 450]	2.14 (1.72–2.66) 0.02–42.68 [19, 177]	2.26 (1.77–2.87) 0.02–32.08 [18, 192]	0.68 (0.35–1.34) 0.01–21.02 [14, 47]
Brook trout ≥20 cm	2.28 (2.09–2.48) 0.01–38.08 [22, 494]	0.59 (0.49–0.71) 0.01–51.91 [21, 505]	8.32 (7.13–9.72) 0.02–33.89 [19, 208]	3.64 (3.10–4.29) 0.01–35.94 [17, 242]
		Sauterelle Lake		
Resource	0.12 (0.10–0.14) 0.01–20.89 [9, 264]	0.13 (0.10–0.16) 0.01–29.79 [9, 183]	0.09 (0.07–0.10) 0.01–12.31 [9, 177]	0.08 (0.08–0.09) 0.01–33.90 [9, 494]
Brook trout <20 cm	1.29 (1.13–1.46) 0.05–100.00 [12, 164]	2.70 (2.06–3.53) 0.04–46.43 [21, 131]	3.11 (2.27–4.26) 0.08–31.52 [12, 96]	0.32 (0.20–0.52) 0.03–20.98 [10, 69]
Brook trout ≥20 cm	1.55 (1.35–1.78) 0.01–124.46 [20, 260]	7.26 (4.72–11.18) 0.07–93.04 [17, 74]	2.58 (1.98–3.37) 0.02–18.98 [14, 129]	0.98 (0.72–1.35) 0.03–37.02 [17, 152]
White sucker <20 cm	0.12 (0.12–0.13) 0.01–12.03 [22, 1150]	0.10 (0.10–0.11) 0.01–9.03 [19, 866]	0.09 (0.08–0.10) 0.01–3.28 [19, 709]	0.09 (0.08–0.10) 0.01–3.75 [19, 344]
White sucker ≥20 cm	0.28 (0.26–0.29) 0.01–18.62 [26, 2154]	0.15 (0.15–0.16) 0.01–27.73 [19, 2061]	0.15 (0.14–0.15) 0.01–28.26 [21, 2680]	0.19 (0.19–0.20) 0.01–21.22 [19, 4903]

TABLE 4. Total number of main benthic organisms per square metre found in the littoral zone (0–2 m depth) of Lakes Vautour and Sauterelle from May to August 1985. Geometric mean weight of organisms (mg dry weight·m^{-2}) in parentheses. *Significant difference in the abundance of organisms between Lake Vautour and Lake Sauterelle (as determinated by the Mann–Whitney U-test, $P < 0.05$); ** significant difference between Lake Vautour and Lake Sauterelle as determinated by a t-test, $p < 0.05$).

	May		June		July		August	
Taxon	Vautour	Sauterelle	Vautour	Sauterelle	Vautour	Sauterelle	Vautour	Sauterelle
Gammaridae	823*	168	255	115	120*	164	1069	443
	(0.21)	(0.12)	(0.35)	(0.16)	(0.28)	(0.12)	(0.07)	(0.09)
Diptera								
Ceratopogonidae	104	10	50	14	76	29	55	5
	(0.22)	(0.18)	(0.13)	(0.16)	(0.14)	(0.10)	(0.18)	(0.05)
Chironomidae	2476*	861	1074	447	1248	582	2121	1741
	(0.13)	(0.12)	(0.10)	(.08)	(0.14)	(0.07)	(0.11)	(0.07)
Other larvae	9	5	13	5	—	—	2	—
	(2.36)	(3.24)	(1.54)	(0.44)			(3.26)	
Diptera pupae	212*	63	56	24	31	29	66	10
	(0.12)	(0.07)	(0.08)	(0.05)	(0.17)	(0.17)	(0.09)	(0.35)
Trichoptera	65	34	50	24	13	—	64	91
	(0.88)	(0.17)	(0.75)	(0.15)	(0.70)		(0.16)	(0.11)
Sialidae	4	—	11	—	8	—	9	24
	(1.39)		(0.92)		(0.88)		(1.70)	(0.07)
Ephemeroptera	74	87	78	245	48	34	30	24
	(0.45)	(0.38)	(0.85)	(0.26)	(5.60)	(0.58)	(0.48)	(0.40)
Odonata	87	43	37	5	46	14	87	38
	(1.53)	(4.27)	(1.58)	(29.79)	(2.33)	(4.32)	(1.09)	(4.31)
Mean density (no.·m^{-2} ± 1 SE)[a]	3853** ±615	1270 ±163	1623 ±366	880 ±212	1589 ±299	851 ±149	3501 ±411	2376 ±244
Relative biomass (g·m^{-2}) ± 1 SE)[a]	1.85** ±0.39	0.69 ±0.33	1.20 ±0.23	0.69 ±0.19	1.41** ±0.28	0.28 ±0.06	1.03 ±0.20	0.78 ±0.30
No. of samples	10	9	20	9	17	9	19	9

[a]Actual data are presented but analyses were performed on transformed data.

TABLE 5. Mean water temperature (°C) from surface to 4-m depth in Lakes Vautour and Sauterelle from May to August 1985.

Depth (m)	May	June	July	August
0.5	14.5	18.0	22.1	22.5
1.0	14.5	17.9	22.1	22.5
1.5	14.5	17.8	22.1	22.5
2.0	14.5	17.8	21.8	22.3
2.5	13.8	17.4	21.5	22.1
3.0	11.8	17.1	21.0	21.5
3.5	10.5	16.0	18.8	20.5
4.0	8.5	14.4	17.0	19.4

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Exhaustive Exercise in "Wild" Atlantic Salmon (*Salmo salar*): Acid–Base Regulation and Blood Gas Transport

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Tufts, B. L., Y. Tang, K. Tufts, and R. G. Boutilier. 1991. Exhaustive exercise in "wild" Atlantic salmon (*Salmo salar*): acid–base regulation and blood gas transport. Can. J. Fish. Aquat. Sci. 48: 868–874.

Wild Atlantic salmon (*Salmo salar*) collected during their spawning migration were transported to the laboratory to investigate effects of exhaustive exercise on acid–base regulation and blood gas transport. Exhaustive exercise resulted in a very large extracellular acidosis which lasted for about 4 h. Blood lactate levels were extremely high and remained significantly elevated for at least 8 h after exercise. The degree of erythrocyte pH regulation was minimal and there was a significant fall in both erythrocyte pH and hemoglobin:oxygen carriage during the recovery period. Together, the significant decrease in erythrocyte pH and a significant reduction in the arterial partial pressure of oxygen resulted in a significant fall in arterial oxygen content immediately after exercise. Thereafter, arterial oxygen content was maintained by a significant increase in hematocrit and an increase in the arterial partial pressure of oxygen. Despite the extremely large lactacidosis in these wild fish, there were no mortalities during the recovery period. However, significant mortality has been reported in studies on domestic salmonids, and this suggests that wild salmonids may be better adapted for exhaustive exercise. This result supports the rationale of a "catch and release" recreational fishery for Atlantic salmon.

On a soumis en laboratoire des saumons de l'Atlantique (*Salmo salar*), recueillis durant leur migration de fraie, à un effort physique important pour en étudier les effets sur la régulation acido-basique et le transport sanguin des gas. L'effort a provoqué chez les saumons une acidose extracellulaire très marquée qui s'est prolongée durant environ 4 h durant la période de repos. Les taux de lactate sanguin étaient très élevés et sont restés supérieurs à la normale au moins 8 h après l'effort. Le degré de régulation du pH érythrocytaire de même que le taux de transport de l'oxygène par l'hémoglobine ont chuté de façon significative au cours de la période de récupération. Les baisses significatives du pH érythrocytaire et de la pression artérielle partielle de l'oxygène se sont traduites par une baisse significative de la concentration artérielle de l'oxygène immédiatement après l'effort. Par la suite, la concentration artérielle de l'oxygène a été maintenue par un accroissement significatif de l'hématocrite et une augmentation de la pression artérielle partielle de l'oxygène. Malgré la lacticémie très marquée observée chez ces poissons sauvages, aucun d'entre eux n'est mort durant la période de récupération. Par ailleurs, les résultats de plusieurs études ont fait état de taux de mortalité importants attribuables à l'effort chez des salmonidés domestiques, ce qui laisse entendre que les salmonidés sauvages résisteraient mieux à un effort important. L'idée d'une pêche récréative du saumon de l'Atlantique où les pêcheurs remettraient leurs prises à l'eau trouve appui dans les résultats de la présente étude.

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The Atlantic salmon (*Salmo salar*) is clearly the most valuable recreational species on the east coast of Canada as well as an important commercial species in some areas. Recent declines in the population of this species over the past several years, therefore, have resulted in legislative action by the federal government to preserve the stocks and attempt to return the population to previous levels. As part of this legislation, recreational fishermen must release all multi-sea winter salmon (i.e. over 63 cm in length) and all smaller salmon over and above the angler's daily or seasonal limit. Thus, a large number of these fish which are ascending rivers on their spawning migration are exercised to complete exhaustion by anglers and then released. Although a number of physiological studies have examined the effects of exhaustive exercise on acid–base balance and blood gas transport in salmonids, the vast majority of these studies have typically been carried out on hatchery stocks of easily domesticated species such as the rainbow trout (*Oncorhynchus mykiss*, formerly *Salmo gairdneri*). To date, there has been no attempt to characterize the physiological disturbance associated with exhaustive muscular activity in *S. salar*. The degree of lactacidosis following exhaustive activity may be quite variable between salmonid species (Heisler 1984). Furthermore, the physiology of exercise-trained fish may be markedly different than that of untrained fish (Johnston 1982; Lackner et al. 1988). Clearly, this suggests that marked physiological differences probably also exist between hatchery and domestic fish stocks. Exercise data on other salmonid species, particularly domestic fish, therefore, may not be directly applicable to wild *S. salar* which is renowned for its capacity for burst activity. Finally, there are reports that exhaustive muscular activity may be associated with delayed mortality in fish (Black 1958; Wood et al. 1983). Thus, a description of the stress associated with exhaustive muscular activity in wild Atlantic salmon would clarify the effects of the present "catch

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and release'' fishery on the physiology of *S. salar*. On this background, the purpose of the present experiments was to characterize the physiological disturbance associated with exhaustive exercise in ''wild'' *S. salar* through a detailed examination of acid–base regulation and blood gas transport.

Materials and Methods

Animals and Rationale

Wild Atlantic Salmon (1.5 ± 0.4 kg; $N = 16$) were collected during their spawning migration in July from the fishladder on the Lahave River in Nova Scotia. The animals were transported to Dalhousie University in Halifax, N.S., where they were held in the aquatron facility at 18°C for at least 1 wk prior to the experiments. Under natural conditions, these animals do not feed during the spawning run, and therefore, no attempt was made to feed the salmon in captivity.

In the wild, Atlantic salmon are exercised to complete exhaustion by anglers, followed by a brief period of handling and their subsequent release. It was not practical to angle these fish in our laboratory setting, but we did make every attempt to reproduce the period of exhaustive exercise and brief handling characteristic of angled fish. In addition, all fish were fitted with a dorsal aortic cannula 48 h prior to the experiment which permitted nonstressful blood sampling of each fish prior to exercise and during the recovery period. This method has clear advantages over ''grab and stab'' techniques of blood sampling which cause the fish to struggle and can influence the acid–base variables followed in this type of study. Thus, our method should provide an accurate description of the magnitude of the disturbance caused by angling in a wild fish and the time course of recovery.

Surgery

To insert the dorsal aortic cannula, the salmon were first anaesthetized in an aerated and pH-balanced solution of tricaine methanesulfonate (MS-222) (66.7 mg MS-222·L^{-1} and 133.3 mg $NaHCO_3 \cdot L^{-1}$. The cannulation was then performed on a surgical table where a lighter dose of the aerated anaesthetic solution (50 mg MS-222·L^{-1} and 100 mg $NaHCO_3 \cdot L^{-1}$) was recirculated over the gills. A cannula of P.E. 50 tubing was implanted in the dorsal aorta using the technique of Smith and Bell (1964). Following surgery, the fish recovered for 48 h in light-proof perspex boxes.

Experimental Protocol

In in vivo experiments, following 48 h of recovery from surgery, a total of 1.5 mL of blood was taken into two 1-mL gas-tight Hamilton syringes. Whole-blood (extracellular) pH (pH_e), carbon dioxide content (C_{CO_2}), oxygen content (C_{O_2}), and the partial pressure of oxygen (P_{O_2}) were measured immediately using 300 μL of the sample. Duplicate hematocrit measurements were made on 150 μL of blood. The C_{CO_2} of true plasma was determined on a 50-μL sample of plasma from the hematocrit tubes. Two 100 μL fractions of the original sample were each added to 200 μL of chilled 8% perchloric acid (PCA) for the subsequent determination of whole-blood lactate and nucleotide triphosphate (NTP) concentrations, respectively. The samples for NTP were centrifuged and the supernatant was stored in liquid nitrogen until further analysis. The lactate samples were stored in the refrigerator (4°C). In addition, duplicate 25-μL samples of whole blood were each added to 5 mL of Drabkin's reagent for the determination of hemoglobin (Hb) concentration. The remaining sample was centrifuged in a 1.5-mL eppendorf tube. The supernatant and the buffy coat from the erythrocytes were removed and the erythrocyte pellet was immediately frozen in liquid nitrogen for the subsequent determination of erythrocyte pH (pH_i).

After the control sample was taken, the salmon was moved to a cylindrical tank (1.5-m in diameter) where it was exhaustively exercised by manual chasing. The exercise period was terminated after about 10 min when the salmon rolled on its side and would no longer respond to chasing. The exhausted fish was then returned to the perspex container and another 1.5-mL blood sample was removed. Analyses similar to those described for the control sample were performed on this blood sample. Samples were also taken at 0.5, 1, 2, 4, 8, and 24 h of recovery from exercise. Throughout the experiment, blood samples were replaced with a similar volume of Cortland saline. This protocol was repeated on six of the salmon. As a control, an identical sampling protocol was performed on an additional four salmon which were not exhaustively exercised.

Further analysis of the characteristics of wild Atlantic salmon blood was carried out in vitro. The first series of in vitro experiments was conducted to determine the in vitro gas transport properties of the blood. In these experiments, 3-mL blood samples were removed from resting cannulated salmon and equilibrated in an intermittently rotating glass tonometer. The blood was equilibrated for 30 min with a humidified 0.2% CO_2–air mixture at 18°C. Following equilibration, a 1-mL blood sample was removed with a gas-tight Hamilton syringe. pH_e, C_{CO_2}, C_{O_2}, and Hb concentration were determined immediately and the remainder of the sample was centrifuged. The resulting supernatant was discarded and the erythrocyte pellet was frozen in liquid nitrogen for the determination of pH_i. This procedure was also repeated on the same blood pool with humidified 1 and 3% CO_2–air mixtures.

Another series of in vitro experiments examined the effects of adrenergic stimulation on the pH gradient across the membrane of salmon red blood cells. This time, 4-mL blood samples were removed from resting cannulated salmon ($N = 6$) and equilibrated with a humidified 1% CO_2–air mixture in paired intermittently rotating tonometers at 18°C with 2mL of blood per tonometer. Following a 30-min equilibration period, a 1-mL blood sample was removed from each tonometer and analysed for pH_e and pH_i. At this point, 100 μL of either saline (sham) or isoproterenol (final concentration 10^{-5} M) in saline was added to each blood pool. The blood was then equilibrated for a further 15 min at which time the final 1 mL of blood was removed for the determination of pH_e and pH_i.

In the final series of in vitro experiments, we investigated the effects of adrenergic stimulation on the aerobic metabolism of salmon red blood cells. In this series, 3-mL blood samples were removed from resting cannulated salmon ($N = 6$) and equilibrated with a humidified 1% CO_2–air mixture in paired tonometers at 15°C with 1.5 mL of blood per tonometer. Following a further 10 min of equilibration, a 1-mL blood sample was removed from each tonometer with a 1-mL gas-tight Hamilton syringe. Determinations of C_{CO_2}, C_{O_2}, and Hb concentration were made immediately on 250 μL of blood. The remaining blood was equilibrated within the gas-tight syringe over a 4-h period at 15°C in a constant-temperature room. Samples from the syringe were also taken after 2 and 4 h for similar analyses. Together, these three samples were used to determine

erythrocyte oxygen consumption and carbon dioxide production rates. It should be noted that this final series was carried out at 15°C rather than 18°C to facilitate direct comparison of aerobic metabolism with data from other studies.

Analyses

pH_e and pH_i were determined with a PHM 84 pH meter and associated micro-pH unit (Radiometer, Copenhagen, Denmark) at 18°C. Erythrocyte samples were frozen and thawed twice in liquid nitrogen prior to the determination of pH according to the method of Zeidler and Kim (1977). The P_{O_2} of whole blood was measured with an E5046 oxygen electrode (Radiometer, Copenhagen, Denmark) at 18°C. Another E5046 oxygen electrode was used to determine the C_{O_2} of whole blood samples using the Tucker method (Tucker 1967). Analysis of Hb concentrations was performed by the Drabkin's method with Sigma reagents. Total C_{CO_2} of whole blood and plasma were measured with a Carle Series 100 gas chromatograph (Carle Instruments Inc., USA), as described by Boutilier et al. (1984). Arterial CO_2 tension (Pa_{CO_2}) and plasma bicarbonate concentration ($[HCO_3^-]_{pl}$) were calculated via a rearrangement of the Henderson–Hasselbach equation, using measured values of pH_e and plasma C_{CO_2}. Constants for plasma pK′ and CO_2 solubility to be used in these calculations were obtained from Boutilier et al. (1984). The concentration of metabolic protons added to the whole blood ($[H^+]_m$) over any given time period (e.g. time 1 to 2) was calculated according to McDonald et al. (1989) using the following equation:

$$H^+_m = [HCO_3^-]_{wb,1} - [HCO_3^-]_{wb,2} - B(pH_{e,1} - pH_{e,2})$$

where $[HCO_3^-]_{wb}$ is the whole-blood bicarbonate concentration which was determined using the same calculation described for plasma bicarbonate, the only exception being that whole-blood C_{CO_2} was used rather than plasma C_{CO_2}. The nonbicarbonate buffer value of whole blood (B) was determined from the hemoglobin concentration ([Hb]) according to the following relationship:

$$B = (-1.895\ [Hb]) + 2.251, \quad r = -1.0$$

which was experimentally determined in the second series of experiments. The concentration of lactate was measured using the L-lactate dehydrogenase method (Loomis 1961) using Sigma reagents. The amount of lactate added to the blood over any given time (t) was calculated according to the equation

$$\Delta La^- = [La^-]_t - [La^-]_R$$

where $[La^-]_R$ is the $[La^-]$ at rest.

The proton (H^+) deficit was then obtained by subtracting $[H^+]_m$ from the ΔLa^-.

Statistics

A paired Student t-test was used to compare the resting values with the postexercise values in the in vivo experiments and the pre- and posttreatment erythrocyte values in the in vitro experiments. An unpaired Student t-test was also used to compare the control salmon and the exercised salmon in the in vivo experiments. Finally, an analysis of covariance was used to compare the in vivo and in vitro slopes of the regression lines for pH_e and pH_i. In all cases, $p < 0.05$ was the accepted level of significance.

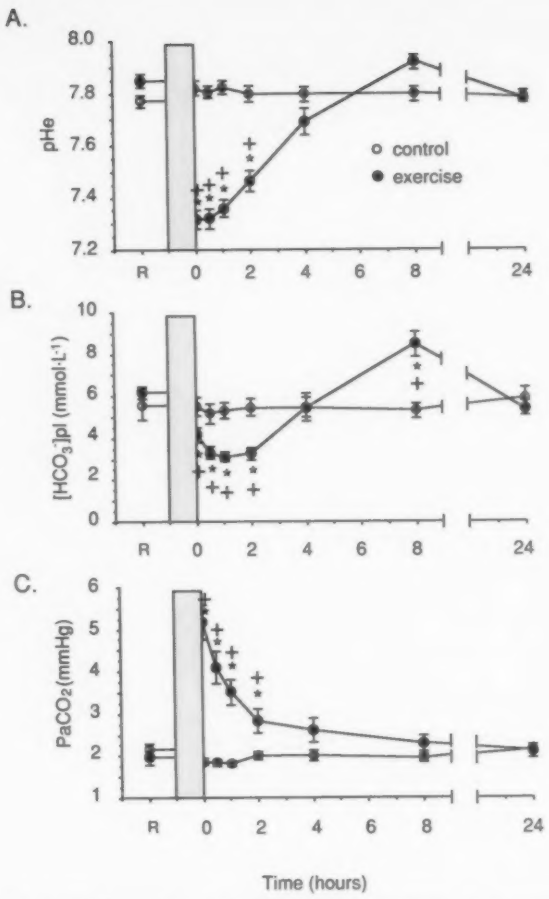

FIG. 1. (A) Extracellular pH (pH_e), (B) plasma bicarbonate concentration ($[HCO_3^-]_{pl}$), and (C) arterial CO_2 tension (Pa_{CO_2}) at rest (R) and 0, 0.5, 1, 2, 4, 8, and 24 h following exhaustive exercise (shaded bar) in *S. salar*. Values are means ± standard error (control, $N = 4$; exercise, $N = 6$). Asterisk denotes significant ($p < 0.05$) difference from resting value; plus sign denotes significant ($p < 0.05$) difference from control value.

Results

Exhaustive exercise in *S. salar* results in a large immediate drop in pH_e from the resting value of 7.848 ± 0.026 to 7.316 ± 0.035 (Fig. 1A). The pH_e remained significantly reduced until the 4-h sample. A similar pattern was also observed in $[HCO_3^-]_{pl}$ which fell significantly from 6.18 ± 0.28 to 4.15 ± 0.34 mmol·L^{-1} immediately after exercise (Fig. 1B). The lowest $[HCO_3^-]_{pl}$ value of 3.13 ± 0.24 mmol·L^{-1} was observed 1 h into the recovery period, and by the 4-h sample, $[HCO_3^-]_{pl}$ had risen to a value which was not significantly different from the resting value. This was followed by an overcompensation in $[HCO_3^-]_{pl}$ at 8 h to 8.46 ± 0.61 mmol·L^{-1}, but at 24 h the value had returned to normal. Pa_{CO_2} increased significantly following the exercise period (Fig. 1C). The greatest increase was observed immediately following exercise when Pa_{CO_2} had risen from 1.97 ± 0.17 mmHg (1 mmHg = 133.322 Pa) at rest to 5.19 ± 0.41 mmHg. Pa_{CO_2} remained significantly elevated until the 4-h recovery sample.

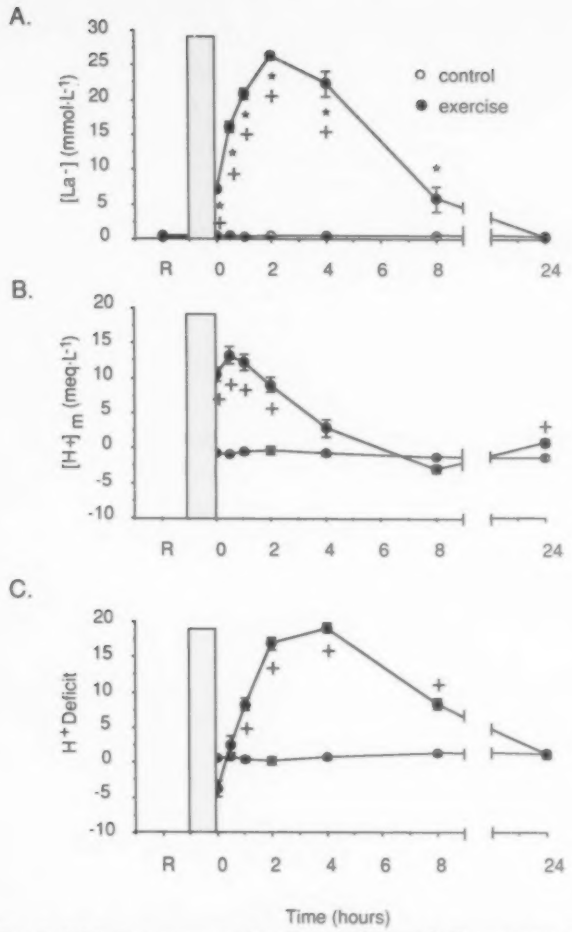

FIG. 2. (A) Lactate concentration ($[La^-]$), (B) metabolic proton load ($[H^+]_m$), and (C) proton deficit at rest (R) and 0, 0.5, 1, 2, 4, 8, and 24 h following exhaustive exercise (shaded bar) in *S. salar*. Values are means ± standard error (control, $N = 4$; exercise, $N = 6$). Asterisk denotes significant ($p < 0.05$) difference from resting value; plus sign denotes significant ($p < 0.05$) difference from control value.

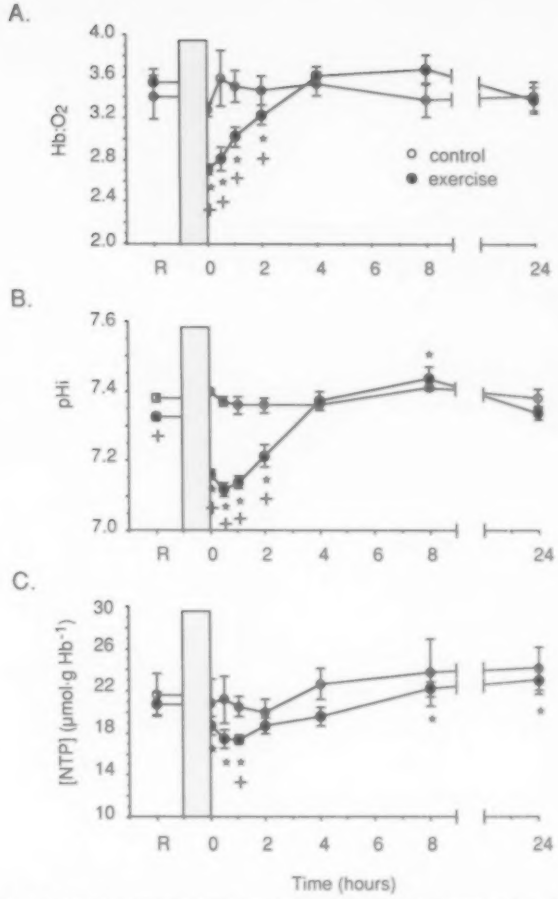

FIG. 3. (A) Hemoglobin:oxygen carriage ($Hb:O_2$), (B) erythrocyte pH (pH_i), and (C) NTP concentration ([NTP]) at rest (R) and 0, 0.5, 1, 2, 4, 8, and 24 h following exhaustive exercise (shaded bar) in *S. salar*. Values are means ± standard error (control, $N = 4$; exercise, $N = 6$). Asterisk denotes significant ($p < 0.05$) difference from resting value; plus sign denotes significant ($p < 0.05$) difference from control value.

Whole blood lactate concentrations $[La^-]$ reached peak levels 2 h after exercise (26.3 ± 0.5 mmol·L^{-1}) and remained significantly higher than the resting value for 8 h (Fig. 2A). $[H^+]_m$, however, peaked at 13.2 ± 1.3 meq·L^{-1} after only 0.5 h and had returned to levels which were no longer significantly different than rest by 4 h (Fig. 2B). Figure 2C plots the proton deficit which is the calculated difference between ΔLa^- and $[H^+]_m$. Immediately following the exercise period, $[H^+]_m$ exceeds ΔLa^- and the proton deficit, therefore, is negative. After 1 h, however, this relationship is reversed. The largest proton deficit of 19.1 ± 0.9 mmol·L^{-1} is observed after 4 h when the $[H^+]_m$ has fallen close to the resting value, but ΔLa^- is still high.

Exhaustive exercise in *S. salar* is associated with a substantial (25%) drop in hemoglobin:oxygen ($Hb:O_2$) carriage (Fig. 3A). Immediately following the exercise period, the significant fall in P_{O_2} could contribute to the change in $Hb:O_2$ (Table 1). The P_{O_2} quickly returns to normal, however, and by 1 h has significantly increased. Thus, the significant decrease in $Hb:O_2$ for the first 2 h of the recovery period is mainly due to the fall in pH_i and the associated reduction in $Hb:O_2$ via the Root effect (Fig. 4). The largest drop in pH_i of 0.210 pH unit occurs after 0.5 h and pH_i remains significantly below the resting value until the 4-h sample (Fig. 3B). At 8 h, there is a significant increase in pH_i, but by 24 h, pH_i had again returned to normal. Concurrent with the fall in pH_i, there is also a significant decrease in erythrocyte NTP levels, which may partially ameliorate the deleterious effects of pH_i on $Hb:O_2$ affinity. Despite the fall in $Hb:O_2$ carriage, arterial oxygen content is only significantly reduced immediately following exercise. By 0.5 h of recovery, there is a significant increase in hematocrit, and oxygen content is thereby preserved. It should be noted that there was no significant difference in mean cellular Hb concentration after exercise, and the increase in hematocrit is therefore probably due to an increase in the number of circulating erythrocytes. A significant reduction in oxygen content is also observed after 8 and 24 h in both the control and exercise animals. This reduction can be attributed to repetitive blood

TABLE 1. Effect of exhaustive exercise on hematocrit, Po_2, and O_2 content (CaO_2) in *S. salar* at 18°C. Values are means ± standard error (control, N = 4; Exercise, N = 6). Asterisk denotes significant ($p < 0.05$) difference from resting value; plus sign denotes significant ($p < 0.05$) difference from control value.

	Rest	0 h	0.5 h	1 h	2 h	4 h	8 h	24 h
Hematocrit (%)								
Control	25.4 ± 3.8	25.2 ± 3.5	24.5 ± 4.7	25.9 ± 3.4	24.2 ± 3.5	21.6 ± 3.5*	20.6 ± 4.8*	19.4 ± 3.4*
Exercise	29.5 ± 2.7	32.7 ± 1.9	38.2 ± 2.1*	37.9 ± 1.4*+	35.6 ± 1.6+	29.9 ± 1.9	21.4 ± 1.9*	20.0 ± 3.0*
Po_2 (mmHg)								
Control	87.2 ± 5.4	86.7 ± 4.9	87.8 ± 3.9	87.9 ± 3.6	90.9 ± 4.7	92.4 ± 4.4	88.0 ± 6.0	81.9 ± 6.1
Exercise	89.4 ± 2.5	77.3 ± 4.0*	84.9 ± 7.3	98.6 ± 3.7*	92.4 ± 4.8	87.5 ± 4.6	95.8 ± 2.3	94.7 ± 4.1
CaO_2 (vol %)								
Control	10.4 ± 1.6	9.7 ± 1.2	10.5 ± 2.4	10.1 ± 1.4	9.8 ± 1.5	8.7 ± 1.4*	8.2 ± 2.0*	8.2 ± 1.4*
Exercise	12.0 ± 0.6	9.7 ± 0.6*	11.6 ± 0.7	12.0 ± 0.6	11.8 ± 0.5	11.5 ± 0.6	9.4 ± 0.7*	8.4 ± 1.1*

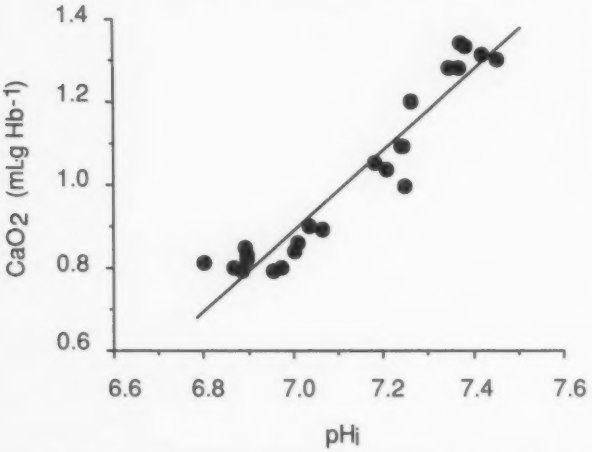

FIG. 4. Relationship between arterial oxygen content (Cao_2) and erythrocyte pH (pH_i) for the blood of *S. salar*. The regression equation describing the relationship is $Cao_2 = (0.952)pH_i - 5.77$, $r^2 = 0.917$.

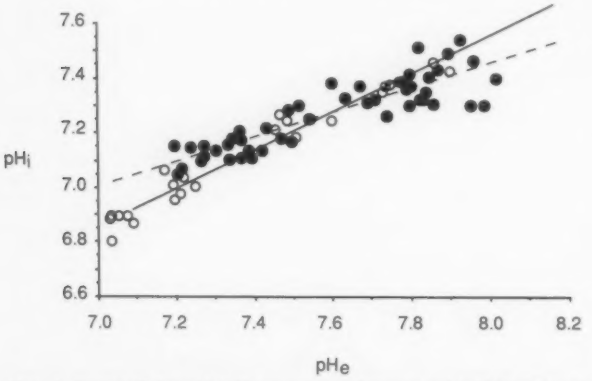

FIG. 5. Extracellular pH (pH_e) versus erythrocyte pH (pH_i) for blood from *S. salar* in vitro (○) and in vivo (●). The regression equation for the in vitro values is $pH_i = (0.696)pH_e + 1.985$, $r^2 = 0.96$ and the equation for the in vivo values is $pH_i = (0.443)pH_e + 3.904$, $r^2 = 0.77$. The lines are significantly ($p < 0.05$) different.

sampling, since it is clearly associated with a significant decrease in hematocrit during the latter stages of the experiment.

The slope of the relationship between pH_e and pH_i in vivo is significantly different from that in vitro (Fig. 5). Thus, below

TABLE 2. Effect of isoproterenol on pH_e, pH_i, and the pH gradient (ΔpH) across the membrane of *S. salar* erythrocytes at 18°C. Values are means ± standard error ($N = 6$). Asterisk denote significant ($p < 0.05$) difference from control value.

	Control	Treatment
Sham		
pH_e	7.411 ± 0.016	7.497 ±0.022*
pH_i	7.214 ± 0.013	7.238 ± 0.007
ΔpH	0.196 ± 0.027	0.260 ± 0.025*
Isoproterenol		
pH_e	7.473 ± 0.023	7.339 ± 0.015*
pH_i	7.234 ± 0.011	7.262 ± 0.011
ΔpH	0.239 ± 0.028	0.076 ± 0.014*

pH_e of 7.6, the pH_i measured in vivo is higher than that measured in vitro. At a pH_e of 7.3, characteristic of the exhausted salmon, this difference in pH_i is equivalent to 0.072 pH unit.

The erythrocytes of *S. salar* are clearly sensitive to adrenergic stimulation in vitro. Addition of isoproterenol results in a significant decrease in the pH gradient across the erythrocyte membrane, indicating transfer of protons from the intracellular to the extracellular compartment (Table 2). Isoproterenol addition also increases the aerobic respiration of the erythrocytes causing a 52% increase in oxygen consumption and a 94% increase in CO_2 production (Fig. 6).

Discussion

Burst activity in salmonids is associated with a marked acidosis due to the large production and release of protons into the extracellular fluid from the poorly perfused white muscle. In wild *S. salar*, this acidosis is most severe during the 2 h immediately following exercise, and by 4 h the pH_e returns very close to normal (Fig. 1). The duration of this extracellular recovery period is very similar to that of burst-exercised rainbow trout (Holeton et al. 1983; Turner et al. 1983; Milligan and Wood 1986a, 1986b; Primmett et al. 1986; Tang et al. 1989; McDonald et al. 1989). However, the magnitude of the disturbance is markedly greater in *S. salar*. As well, the whole-blood lactate concentrations reach much higher values than those frequently reported for other salmonid species (Black 1957a, 1957b; Holeton et al. 1983; Turner et al. 1983; Primmett et al. 1986; Tang et al. 1989; McDonald et al. 1989). Only one study by Black (1957c) on *Oncorhynchus nerka* has reported higher extracellular lactate concentrations, although it should be pointed out that 26% of the fish in this study died

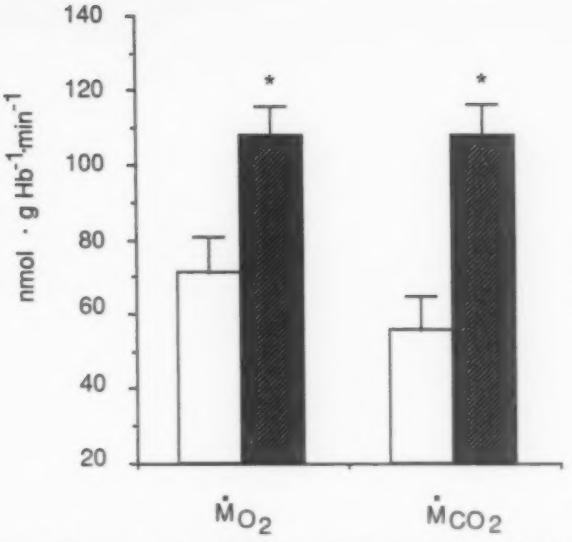

FIG. 6. Oxygen consumption ($\dot{M}O_2$) and carbon dioxide production ($\dot{M}CO_2$) of *S. salar* erythrocytes in vitro under control conditions (open bars) and following addition of isoproterenol (shaded bars). Values are means ± standard error ($N = 6$). Asterisk denotes significant ($p < 0.05$) difference from control value.

during the recovery period. The reason for this variability in reported peak lactate concentrations does not appear to be entirely due to differences in experimental protocol. Indeed, pronounced differences in peak extracellular lactate concentrations following exercise are clearly apparent when broad comparisons are made between fish species (Heisler 1984). Thus, it is reasonable to assume that this variability may also occur to a certain extent within the salmonids.

Oncorhynchus mykiss is the only other salmonid in which $[H^+]_m$ has been determined following exhaustive activity (Milligan and Wood 1986a, 1986b; Tang et al. 1989, McDonald et al. 1989). In comparison, the blood $[H^+]_m$ in the present study is about 50% higher than in the freshwater rainbow trout which is further evidence of a much greater lactacidosis in the Atlantic salmon (Fig. 2B). These metabolic protons, however, disappear from the blood quickly in comparison with extracellular lactate, and therefore, there is a very large proton deficit in our experiments (Fig. 2C). To our knowledge, this is the largest proton deficit ever reported in a fish.

Recently, a great deal of attention has been paid to the importance of pH_i regulation in fish following stresses such as exhaustive activity when there are large perturbations in pH_e (Nikinmaa et al. 1984; Primmett et al. 1986; Milligan and Wood 1986a, 1986b; McDonald et al. 1989). Adrenergic regulation of pH_i under these circumstances can offset the reduction in oxygen carrying capacity associated with the Root effect. The magnitude of this pH_i regulation, however, is quite variable, even within a singles species, and can range from an entire lack of pH regulation (Nikinmaa and Jensen 1986) to complete regulation (Primmett et al. 1986; Nikinmaa and Jensen 1986). The significant fall in pH_i of 0.21 pH unit 30 min after exercise persisted until the 4-h sample when pH_e had recovered to almost normal values (Fig. 3B). *Salmo salar* blood has a significant Root effect, and this fall in pH_i was, therefore, associated with a simultaneous decrease in $Hb:O_2$ carriage (Fig. 3A and 4). When the relationship between pH_e and pH_i observed in vivo was compared with that in vitro, it is clear that there was a minimal, but significant, degree of pH_i regulation despite the fall in pH_i (Fig. 5). At a postexercise pH_e of 7.3, the pH_i in vivo was, in fact, 0.072 pH unit higher than that observed in vitro. Thus, from the Root effect data, it is possible to calculate that this degree of pH_i regulation would result in only a 7% increase in arterial blood $Hb:O_2$ carriage; the latter fell by about 25% following exercise. This decrease in arterial blood $Hb:O_2$ carriage may, in fact, have been even greater had there not been a significant drop in erythrocyte NTP levels at this time which would tend to increase the affinity of Hb for oxygen (Fig. 3C). The reason for the minimal degree of adrenergic pH_i regulation in the present study is not readily apparent. The erythrocytes are clearly sensitive to adrenergic stimulation in vitro (Table 2; Fig. 6). It is possible, however, that several factors might be contributing to the minimal response in vivo. One explanation could be the relative age of the circulating erythrocytes in migrating salmon. During their spawning migration, Atlantic salmon do not feed, and this would be expected to increase the mean age of the circulating erythrocytes, since erythropoietic activity is reduced during periods of starvation (Lane and Tharp 1980). The spleen may release a certain number of younger cells into the circulation following exercise (Wells and Weber 1990). The mean age of the entire circulating population of erythrocytes in migrating salmon, however, is probably older than in feeding fish. Aging in nucleated erythrocytes is also associated with a decrease in oxygen consumption (Tipton 1933). Thus, further evidence of a preponderance of "older" erythrocytes is provided by the observation that resting levels of erythrocyte oxygen consumption in the present experiments are less than half the value for erythrocytes from well-fed domestic *S. salar* (Ferguson and Boutilier 1988). According to Cossins and Kilbey (1989), the Na^+/H^+ exchange activity which drives the pH regulatory response is reduced in older erythrocytes. Together, this evidence suggests that the adrenergic pH response may be reduced in the erythrocytes of migrating salmon due to the greater mean age of the circulating erythrocytes in these starving animals. A further contributing factor to the apparently minimal pH response may also be the severe acidosis following exercise in these animals. Borgese et al. (1987) have demonstrated that a large concentration of external protons may inhibit the activity of the Na^+/H^+ exchanger. Regardless, the present results demonstrate that adrenergic regulation of pH_i probably provides only a minimal benefit to oxygen transport following exhaustive activity in migrating wild Atlantic salmon.

Despite the fall in $Hb:O_2$ carriage in exhausted salmon, arterial oxygen content was constant during the recovery period (Table 1). This regulation was not apparent immediately following the exercise period when the fall in $Hb:O_2$ carriage combined with a drop in P_{O_2} to reduce the content of oxygen. After 30 min, however, there was an increase (30%) in hematocrit, and P_{O_2} had returned to normal. Together these changes combined to offset the reduction in arterial $Hb:O_2$ carriage and preserve arterial oxygen content during the recovery period. Although a decrease in plasma volume after exercise will contribute somewhat to the increase in hematocrit, adrenergic stimulation of the spleen can substantially increase the number of circulating erythrocytes (Nilsson and Grove 1974). Our results suggest that the contribution of the spleen towards the regulation of oxygen content is probably more important than the regulation of pH_i following exhaustive exercise in migrating Atlantic salmon.

There are several reports of delayed mortality associated with exhaustive muscular activity in fish (Black 1957c, 1958; Beggs et al. 1980; Wood et al. 1983). Clearly, a significant mortality in exhausted fish could have important implications for the management of a "catch and release" fishery such as that now in existence for Atlantic salmon. Early reports suggested that this delayed mortality was due to an excessive lactacidosis in the blood, but according to Wood et al. (1983), the probable cause of delayed mortality is the intracellular acidosis associated with the exercise. In this regard, it is important to note that there were no mortalities amongst the wild Atlantic salmon in the present experiments even though the extracellular metabolic acidosis was much greater than that reported in studies where significant delayed mortality was observed. Thus, the present study supports the view that the degree of extracellular acidosis is probably not the cause of death in exhausted fish. Furthermore, on the basis of the present results, we submit that wild fish may not be as prone to delayed mortality following exhaustive exercise as hatchery stocks due to differences in both physiology and selective pressures between hatchery and wild stocks which probably impart a greater level of overall fitness for exhaustive activity amongst the wild species.

In summary, there is a very large metabolic acidosis associated with exhaustive muscular activity in wild Atlantic salmon which persists for at least 2 h into the recovery period. Extracellular lactate concentration levels are also higher than those commonly observed in salmonids, and removal of extracellular lactate is much slower than the recovery from the extracellular acidosis. Thus, we report a larger proton deficit than previously described in salmonids. There is a fall in arterial oxygen content immediately following exercise due to a significant fall in both Po_2 and pH_i which together decrease arterial $Hb:O_2$ carriage. Thereafter, oxygen content is preserved despite the fall in pH_i by a large increase in hematocrit and an increase in Po_2. Even though there was a large metabolic acidosis in these fish, there were no mortalities observed in this study. This supports the view that the extracellular lactacidosis is probably not the cause of delayed mortality in exhausted fish. Furthermore, the absence of mortalities suggests a higher overall level of fitness for burst activity in wild *S. salar* than in domestic salmonids. Finally, the present results support the rationale for a "catch and release" recreational fishery for wild Atlantic salmon.

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2,3,7,8-Tetrachlorodibenzo-*p*-dioxin (TCDD) Toxicity during Early Life Stage Development of Lake Trout (*Salvelinus namaycush*)

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Lake trout (*Salvelinus namaycush*) eggs containing [^{3}H]TCDD concentrations from 0 to 302 parts per trillion (ppt) were observed through the fry stage for TCDD metabolism, elimination, and toxicity. All radioactive residues extracted from eggs and sac fry were due to TCDD; no metabolites were detected. [^{3}H]TCDD was not eliminated from eggs and sac fry, but was rapidly eliminated from fry ($t_{1/2}$, 35–37 d). Hatchability was less at egg TCDD concentrations ⩾226 ppt; however, the greatest TCDD-related mortality occurred during the sac fry stage. In all TCDD groups (34–302 ppt), sac fry that died developed subcutaneous yolk sac edema prior to death, resembling blue-sac disease. The development of yolk sac edema preceded sac fry mortality, and the severity of edema varied directly with cumulative mortality. Based on TCDD concentrations in the egg resulting from a 48-h exposure, the no observable adverse effect level (NOAEL) for mortality was 34 ppt and the lowest observable adverse effect level (LOAEL) was 55 ppt. The TCDD concentration in eggs that caused 50% mortality above control at swim-up (LD_{50}) was 65 ppt. Lake trout sac fry exposed as eggs are more sensitive to the lethal effects of TCDD than any mammalian, avian, or fish species investigated thus far.

Nous avons placé sous observation des oeufs de touladi (*Salvelinus namaycush*) contenant différentes concentrations de [^{3}H]TCDD, variant de 0 à 302 parties par trillion (ppt), jusqu'au stade d'alevin afin d'étudier le métabolisme, l'élimination et la toxicité du TCDD. Tous les résidus radioactifs extraits des oeufs et des alevins vésiculés étaient du TCDD; aucun métabolite n'a été détecté. Les oeufs et les alevins vésiculés n'ont pas éliminé de [^{3}H]TCDD, mais les alevins l'ont éliminé rapidement ($t_{1/2}$ = 35 à 37 jours). Le taux d'éclosion était réduit quand les oeufs contenaient 226 ppt ou plus de TCDD; cependant, la plus forte mortalité a été observée chez les alevins vésiculés. À toutes les concentrations de TCDD (34 à 302 ppt) les alevins vésiculés qui sont morts ont d'abord développé un oedème sous-cutané de la vésicule vitelline, rappelant l'hydropisie du sac vitellin. L'apparition de l'oedème de la vésicule vitelline a précédé celle de la mortalité des alevins vésiculés, et la gravité de l'oedème variait en raison directe de la mortalité cumulative. À partir des concentrations de TCDD dans les oeufs, obtenues par exposition de ces derniers à cette substance durant 48 h, on a établi que la concentration maximale où aucun effet létal n'est observé était de 34 ppt tandis que la concentration la plus basse ayant un effet létal observable était de 55 ppt. La concentration de TCDD dans les oeufs entraînant, au stade où les alevins nagent librement, une mortalité de 50 % supérieure à celle du groupe témoin (DL_{50}) était de 65 ppt. Aucun des mammifères, oiseaux ou autres poissons étudiés à ce jour n'est aussi sensible aux effets létaux du TCDD que les alevins vésiculés de touladi issus d'oeufs qui ont été exposés à cette substance.

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In the 1940s, lake trout (*Salvelinus namaycush*) populations in the Great Lakes were decimated by overfishing, sea lamprey (*Petromyzon marinus*) predation, and degradation of prime spawning habitat, and by the mid-1950s, lake trout were deemed extinct throughout the Great Lakes except for isolated populations in Lake Superior (Wells and McLain 1973). Despite extensive restocking and successful reestablishment of adult lake trout in the Great Lakes, little evidence of natural reproduction exists. Stocked lake trout reach sexual maturity, produce viable gametes, and successfully spawn; however, only negligible numbers of their young survive (Jude et al. 1981; Nester and Poe 1984; Marsden et al. 1988).

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Significant mortality has been documented during lake trout early development from contaminated regions of the Great Lakes (Mac et al. 1985), and the presence of persistent environmental contaminants has been proposed to explain this early life stage mortality (Willford et al. 1981; Mac et al. 1988). Specifically, the combined presence of polychlorinated dibenzo-*p*-dioxins (PCDDs), polychlorinated dibenzofurans (PCDFs), and polychlorinated biphenyls (PCBs) in feral lake trout eggs may be causing poor survival of lake trout during early development and, ultimately, be reducing lake trout reproductive success in the Great Lakes (Walker and Peterson 1990).

PCDDs, PCDFs, and PCBs belong to a family of lipophilic halogenated aromatic hydrocarbons that resist chemical and biological degradation, persist in the environment, and readily bioaccumulate in the food chain (Hutzinger et al. 1985; Tanabe 1988). There are 75, 135, and 209 possible congeners (molecules with different chlorine substitution patterns) of the PCDDs, PCDFs, and PCBs, respectively (Poland and Knutson 1982). However, only 21 congeners are considered extremely toxic (Safe et al. 1985; Environmental Protection Agency (EPA) 1989), and these have chemical structures similar to 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD) (Poland and Knutson 1982). TCDD is the most potent and extensively studied of the halogenated aromatic hydrocarbons and thus serves as a prototype for the other toxic PCDD, PCDF, and PCB congeners (Poland and Knutson 1982).

In the Great Lakes, halogenated aromatic hydrocarbons have bioaccumulated in adult lake trout (Stalling et al. 1983; Schmitt et al. 1985; Huckins et al. 1988; DeVault et al. 1989; Niimi and Oliver 1989; Zacharewski et al. 1989) and have been detected in their eggs (Niimi 1983; Mac et al. 1985; P. Cook and K. Lodge, USEPA, 6201 Congdon Blvd., Duluth, MN 55804, pers. comm.). The major route of halogenated aromatic hydrocarbon accumulation in feral lake trout eggs is not from contaminated lake water; rather, these lipophilic contaminants are directly deposited from the sexually mature adult female lake trout into the eggs prior to spawning (Guiney et al. 1979; Niimi 1983).

Since little information existed on the effects of PCDDs, PCDFs, and PCBs in lake trout eggs during early development, we investigated the toxicity of these contaminants on the development and survival of early life stages of lake trout using TCDD as a prototype.

Material and Methods

[^{3}H]TCDD

[1,6-^{3}H]TCDD (specific activity 16.8 Ci/mmol, 1 Ci = 37 GBq) was obtained from Chemsyn Science (Lenexa, KA) and purified to a final radiochemical purity of >99% by reverse-phase high-performance liquid chromatography (HPLC) as described by Olson (1986).

Lake Trout Eggs

Fertilized eggs were obtained from a naturally reproducing population of lake trout collected by gill nets off Gull Island Shoal in Lake Superior by the Wisconsin Department of Natural Resources in October 1987. Eggs were obtained by manually spawning 28 females and were fertilized with milt from 113 males. Within 4 h after fertilization the eggs (egg number estimated by volume displacement) were divided into 24 subgroups (1300 eggs per subgroup) which were randomly assigned to one of six treatment groups (four subgroups per treatment group). Each subgroup was treated as one replicate.

Background Concentrations of PCDDs and PCDFs in Lake Trout Eggs

Concentrations of individual dioxin and furan congeners in these lake trout eggs were measured using gas chromatography and mass spectroscopy (GC/MS) analysis (EPA 1984). The concentration of TCDD in the eggs was below the limit of detection (0.7 parts per trillion (ppt)), and the only toxic dioxin or furan congener detected in the lake trout eggs was 2,3,7,8-tetrachlorodibenzofuran (TCDF) at a concentration of 2.3 ppt (P. Cook and K. Lodge, op. cit.).

Static Water Exposure of Lake Trout Eggs to [^{3}H]TCDD

Between 4 and 7 h after fertilization, each replicate of approximately 1300 eggs was statically exposed for 48 h to 2.6 L of water containing 0.08 mL of acetone (solvent control) or [^{3}H]TCDD dissolved in 0.08 mL of acetone. Five nominal water concentrations of [^{3}H]TCDD were used: 10, 20, 40, 62, or 100 ppt (ng [^{3}H]TCDD/L water). Throughout the static exposure, the exposure water (7–9°C) was aerated and renewed three times at approximately 12-h intervals with 2.6 L of water containing the appropriate concentration of acetone or [^{3}H]TCDD in acetone. Following the 48-h exposure, eggs from each replicate were transferred to a perforated egg tray and placed in a glass aquarium (38-L capacity) with flowing [^{3}H]TCDD-free water for the remainder of the study.

Maintenance of Lake Trout Eggs, Sac Fry, and Fry

Eggs, sac fry, and fry were maintained in dechlorinated tap water that was [^{3}H]TCDD free (8–12 replacements per day, 8 ± 0.5°C, dissolved oxygen 10.3 ppm, pH 7.5, hardness 136 ppm as $CaCO_3$). Beginning at swim-up, fry were fed Silver Cup® salmon starter diet (52% protein, 14% fat, 12% ash, 3% fiber; Murray Elevator, Murray, UT) at 7% of body weight per day, equally divided among three feedings, until termination of the experiment (60 d post swim-up).

Serial Measurements in Eggs, Sac Fry, and Fry

At designated times after [^{3}H]TCDD exposure, 10 individual eggs (days 3, 31, and 52 postexposure), sac fry (days 66, 87, 105, and 119 postexposure), or fry (days 138, 164, and 174 postexposure) were sampled from each replicate to determine weight, length, and concentration of [^{3}H]TCDD. To determine wet weight, five individual eggs, sac fry, or fry were blotted to remove water from the surface of the organism and weighed; total length of sac fry and fry were measured with a caliper. The remaining five eggs, sac fry, or fry from each replicate were blotted, weighed, and stored at −20°C for subsequent determination of TCDD-derived ^{3}H.

To assess cumulative mortality in each replicate, dead eggs, sac fry, or fry were removed and the number dead recorded daily. At the termination of the experiment (60 d post swim-up), surviving fry in each replicate were counted. Cumulative mortality was calculated excluding the viable eggs, sac fry, and fry which were removed for serial measurements.

Determination of TCDD-derived ^{3}H in Eggs, Sac Fry, and Fry

Frozen samples of eggs, sac fry, or fry (five per replicate) were ground to a homogeneous powder with liquid nitrogen

cooling. Between 140 and 160 mg of the ground sample was weighed and added to 2 mL of Soluene 350 (Packard Instrument Co., Downers Grove, IL) and solubilized at 50°C overnight. The solubilized samples were cooled, 10 mL of Hionic (Packard) liquid scintillation medium added, and low-energy chemiluminescence was allowed to decay prior to estimating counts per minute (cpm) of TCDD-derived ^{3}H by liquid scintillation counting (Packard, model 2000 CA). Using appropriate quench corrections, disintegrations per minute (dpm) were calculated from cpm and counting efficiency. From dpm [^{3}H]TCDD/g egg, sac fry, or fry and [^{3}H]TCDD specific activity (115 dpm/pg [^{3}H]TCDD), the concentration of [^{3}H]TCDD in individual eggs, sac fry, and fry was determined and expressed as picograms [^{3}H]TCDD per gram wet weight (ppt). The limit of detection was 2.1 pg [^{3}H]TCDD (240 dpm)/140 mg solubilized tissue.

Characterization of [^{3}H]TCDD Residues in Eggs and Sac Fry

Lake trout eggs or sac fry, pooled from the four replicates of the highest [^{3}H]TCDD treatment group and sampled 31 and 87 d postexposure, respectively, were quantitatively extracted with ethyl acetate and dried under nitrogen. The extract was dissolved in methanol and analyzed by HPLC using an Altex Ultrasphere-ODS (10 mm × 25 cm) column with a 30-min linear gradient elution of 100% water to 100% methanol at a flow rate of 3 mL/min. Fractions of column effluent were collected at 1-min intervals for 50 min and the TCDD-derived radioactivity determined by liquid scintillation counting.

Safety

Effluent water from aquaria containing [^{3}H]TCDD-exposed lake trout was pumped through a series of sealed plastic canister filters to remove waterborne TCDD; efficiency of the filtration system in removing waterborne [^{3}H]TCDD is 100% (Kleeman et al. 1986). The initial filter removed small particulate matter (Silver Screen No. 1, rust and sediment type, 20- to 30-μm pore size, Pargreen Sales Engineering, Addison, IL) and was followed by two charcoal filters which removed TCDD (Aqua Guard T 2XLS, activated charcoal, taste and odor type, Pargreen Sales Engineering). All filters were changed once per month.

Statistical Procedures

The experiment was designed as a randomized, complete block. Weight, length, and mortality data were analyzed by one-way ANOVA with residual plots examined, results expressed as mean ± SE, and Bonferroni's inequalities used to determine significance at $p < 0.005$ (Snedecor and Cochran 1980). Cumulative mortality data at swim-up in each [^{3}H]TCDD replicate were corrected for control mortality (mean 20.4%; 95% confidence interval 12–29%) using Abbott's formula (Abbott 1925; Hewlett and Plackett 1979) and angularly transformed using a continuity correction (Snedecor and Cochran 1980). The TCDD concentration in eggs that caused 50% mortality above control at swim-up (LD_{50}) was determined from the angularly transformed mortality data using least squares regression (Draper and Smith 1981).Since there is uncertainty in control mortality, the 95% confidence interval of the LD_{50} was calculated taking into account the 95% confidence interval for control mortality. The $t_{1/2}$ for whole-body elimination of [^{3}H]TCDD from fry was calculated assuming first-order elimination as $t_{1/2} = \ln 2/k$ where $-k$ is the slope of the least squares regression line of ln [^{3}H]TCDD content of fry versus time.

TABLE 1. [^{3}H]TCDD concentration (ng/L) in exposure water and in fertilized lake trout eggs following a 48-h static waterborne exposure.[a]

Exposure water[b] (ng [^{3}H]TCDD/L)	Lake trout eggs[c] (pg [^{3}H]TCDD/g wet weight)
0	0
10	34
20	55
40	121
62	226
100	302

[a]Initial exposure water was renewed three times at approximately 12-h intervals with water containing the same concentration of acetone or acetone and [^{3}H]TCDD.

[b]Nominal concentration of [^{3}H]TCDD in water.

[c]For each exposure group the concentration of [^{3}H]TCDD in lake trout eggs was equivalent on days 3, 31, and 52 postexposure. Therefore, the concentration of [^{3}H]TCDD in lake trout eggs was calculated as the mean of these three sampling times.

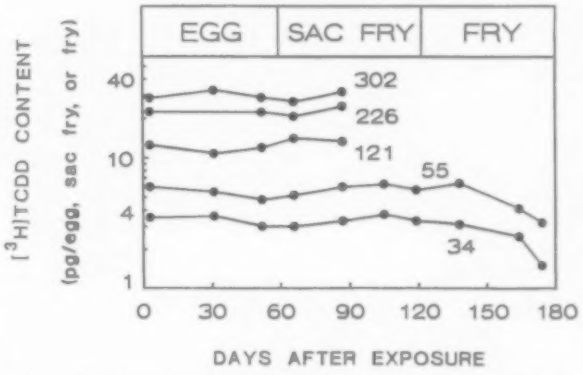

FIG. 1. Absolute amount of [^{3}H]TCDD in individual eggs, sac fry, or fry following exposure of fertilized eggs to waterborne [^{3}H]TCDD. Treatment groups are designated by the mean in vivo concentrations of [^{3}H]TCDD in eggs on days 3, 31, and 52 postexposure. Each point is the mean of four replicates. Cumulative mortality in the 121, 226, and 302 ppt [^{3}H]TCDD groups reached 100% in the mid- to late sac fry stage.

Results

Disposition of [^{3}H]TCDD in Lake Trout Eggs, Sac Fry, and Fry

During the 48-h static waterborne exposure of lake trout eggs to [^{3}H]TCDD, eggs accumulated [^{3}H]TCDD concentrations approximately three times greater than the nominal exposure water concentrations (Table 1). The accumulated concentration of [^{3}H]TCDD remained constant through the egg and sac fry stages of development (data not shown); therefore, the six treatment groups will be designated based on their mean in vivo concentrations of [^{3}H]TCDD in the eggs.

During the egg and sac fry stages of development, the absolute amount of [^{3}H]TCDD in eggs and sac fry was constant with no significant elimination (Fig. 1). However, during the fry stage, the [^{3}H]TCDD content declined in an apparent first-

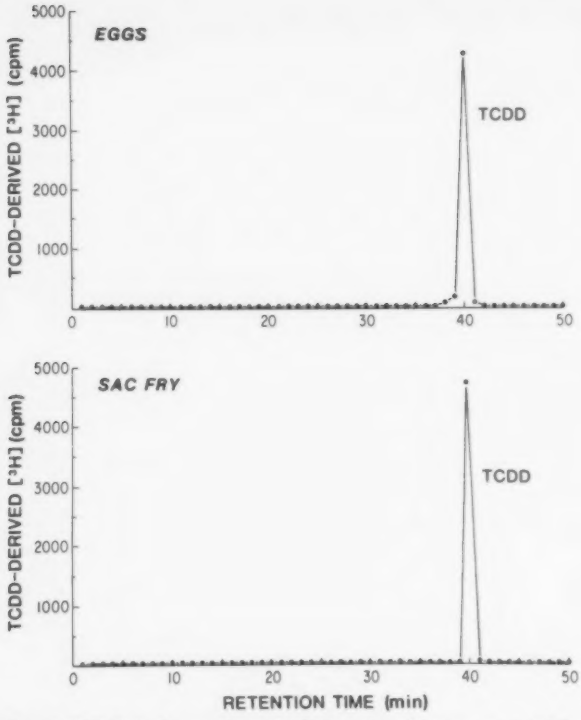

FIG. 2. HPLC elution profiles of TCDD-derived ^3H in extracts of lake trout eggs (top panel) and lake trout sac fry (bottom panel) exposed to [^3H]TCDD as fertilized eggs and sampled 31 and 87 d postexposure, respectively. The single peak observed in both panels is the parent compound which elutes at 40 min under these chromatographic conditions.

order manner. The $t_{1/2}$ for whole-body elimination of [^3H]TCDD from lake trout fry was 35 and 37 d in the 34 and 55 ppt TCDD groups, respectively.

Ethylacetate extracts of radioactivity from lake trout eggs and sac fry, sampled 31 and 87 d postexposure, respectively, were analyzed by reverse-phase HPLC to assess the chemical nature of the TCDD-derived radioactivity. All the TCDD-derived radioactivity in eggs and sac fry eluted as the parent compound with a retention time of 40 min (Fig. 2). No metabolites of TCDD were detected in either developmental stage.

TCDD Toxicity during Lake Trout Early Development

Cumulative mortality of embryos was unaffected by TCDD prior to the onset of hatching. However, hatchability of lake trout eggs was significantly less in the 226 and 302 ppt TCDD groups with 9.2 ± 1.3 and 16.8 ± 4.0% of the embryos dying partially emerged from the chorion (half-hatched), respectively, compared with 1.6 ± 0.1% half-hatched in the control group.

TCDD toxicity was manifested during the sac fry stage of lake trout development by fluid accumulation beneath the yolk sac epithelial membrane and subcutaneous hemorrhages (Fig. 3), resembling blue-sac disease (Spitsbergen et al. 1991).

During the sac fry stage there was a significant egg TCDD concentration-related increase in sac fry wet weight beginning on day 66 and in cumulative mortality beginning on day 87 (Fig. 4). The development of yolk sac edema, reflected by an increase in sac fry wet weight, preceded and paralleled an increase in sac fry mortality, so that sac fry died with severe yolk sac edema. Neither cumulative mortality nor wet weight was affected by TCDD during the fry stage.

The presence of yolk sac edema was an accurate predictor of sac fry mortality. The magnitude of sac fry wet weight (a quantitative index of yolk sac edema) varied directly with cumulative mortality for control and all TCDD groups (Fig. 5).

Relationship between Concentration of TCDD in Eggs and Cumulative Mortality, Sac Fry Wet Weight, and Sac Fry Length

Exposure of lake trout eggs to TCDD resulted in egg TCDD concentration-related increases in cumulative mortality and sac fry wet weight and decreases in sac fry length (Fig. 6). Following a 48-h exposure to [^3H]TCDD, whole-egg TCDD concentrations of 34 ppt did not significantly increase cumulative mortality compared with control and therefore represented a "no observable adverse effect level" (NOAEL) for mortality. The lowest TCDD concentration in eggs that caused a significant increase in mortality was 55 ppt and this represented the "lowest observable adverse effect level" (LOAEL) for mortality (Fig. 6A). The lowest egg TCDD concentration that caused a significant increase in sac fry wet weight was 55 ppt (Fig. 6B), while the lowest egg TCDD concentration that caused a significant decrease in sac fry length was 226 ppt (Fig. 6C). The LD_{50} was 65 ppt (95% confidence interval 60–71 ppt) (Fig. 7).

Discussion

Our research for the first time relates the concentration of TCDD in lake trout eggs to toxicity manifested during early development. Since the developmental toxicity of TCDD in lake trout is manifested by sac fry mortality, elevated concentrations of TCDD in Great Lakes lake trout eggs have the potential to cause poor survival during early development and, ultimately, reduce lake trout reproductive success.

Sensitivity of Early Life Stages of Lake Trout to TCDD

Lake trout sac fry are extremely sensitive to TCDD toxicity when exposed to waterborne [^3H]TCDD as fertilized eggs. Following a 48-h exposure to [^3H]TCDD, an egg TCDD concentration of 34 ppt resulted in NOAEL, while an egg TCDD concentration as low as 55 ppt caused a significant increase in cumulative mortality (LOAEL), and 65 ppt resulted in 50% mortality above control at swim-up. Previous research in our laboratory showed that TCDD concentrations as low as 40 ppt in lake trout eggs significantly increased sac fry mortality (Spitsbergen et al. 1991).

The background concentration of TCDD in these eggs (which were obtained from a naturally reproducing population of lake trout in Lake Superior) was not detectable; the only toxic dioxin or furan congener detected was TCDF at an egg concentration of 2.3 ppt. Since TCDF is 40–60 times less potent that TCDD in producing toxicity in mammalian species (Safe 1987), we assume that TCDF contributed insignificantly to the toxicity of TCDD during lake trout early development in the present study. Since these eggs were obtained from feral Lake Superior lake trout, we cannot overlook the potential presence of other contaminants in eggs such as PCBs, DDE, and toxaphene. It is

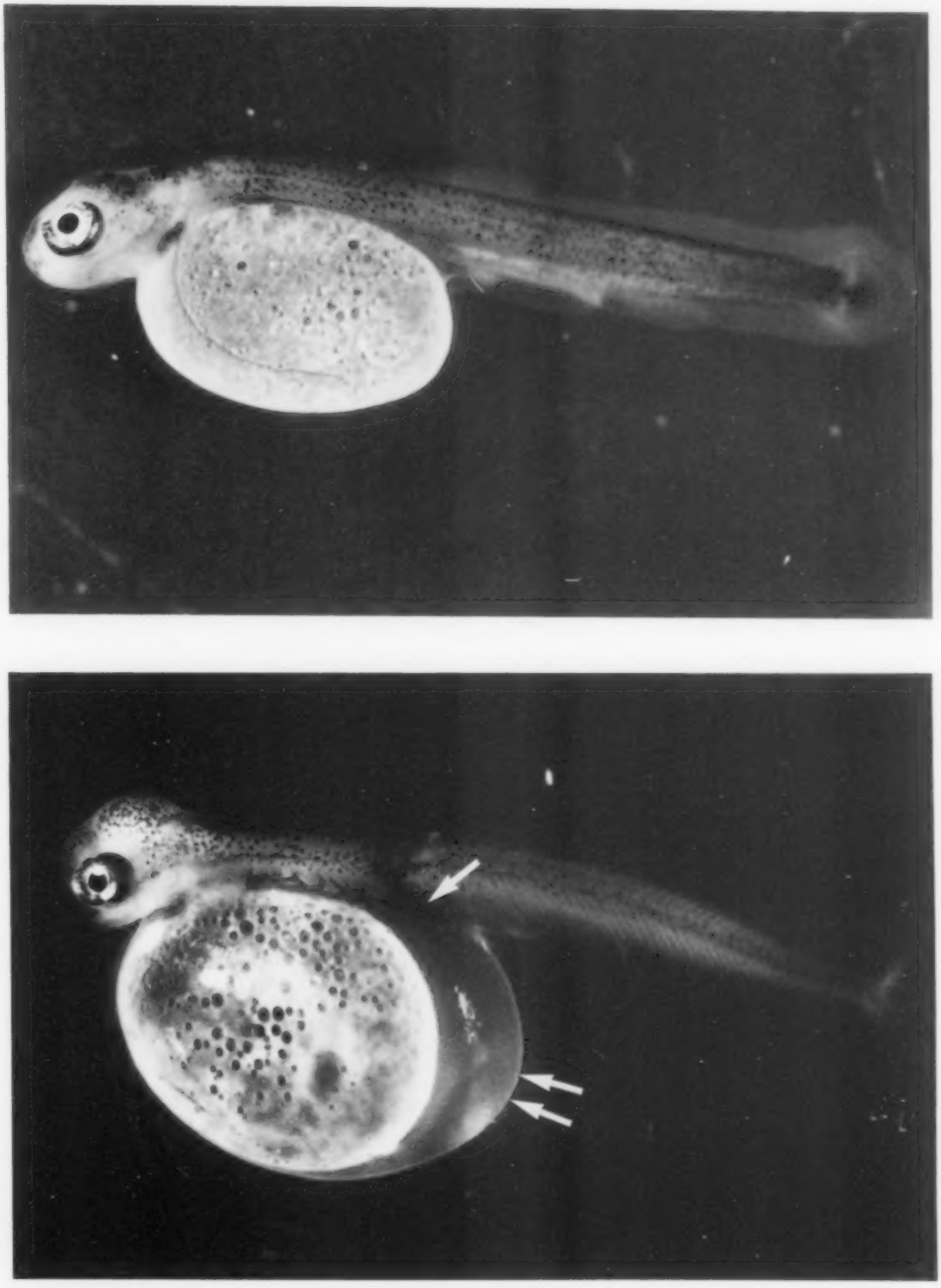

FIG. 3. Representative lake trout sac fry 4 wk posthatch exposed as a fertilized egg to either acetone (top panel) or acetone and [^{3}H]TCDD (bottom panel, egg TCDD concentration = 302 ppt). TCDD toxicity in lake trout sac fry resembles blue-sac disease, with fluid accumulation beneath the yolk sac epithelial membrane (double arrow) and subcutaneous hemorrhages (single arrow). (Reprinted with permission, Spitsbergen et al. 1991)

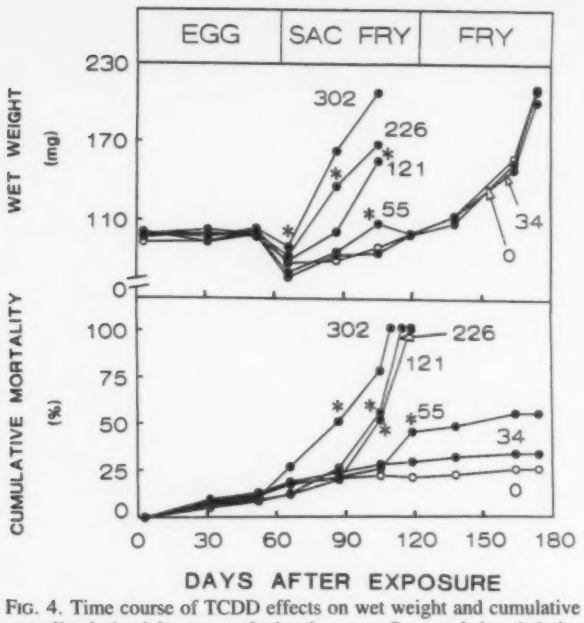

FIG. 4. Time course of TCDD effects on wet weight and cumulative mortality during lake trout early development. Open and closed circles represent acetone control and [^{3}H]TCDD groups, respectively. Significant differences between control and TCDD groups are indicated by an asterisk ($p < 0.005$).

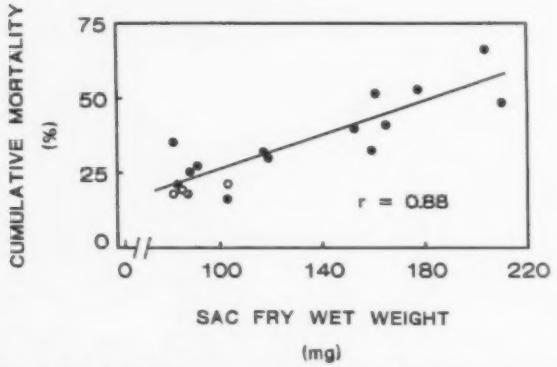

FIG. 5. Relationship between cumulative mortality and sac fry wet weight 105 d after exposure of fertilized eggs to [^{3}H]TCDD ($F = 149.1$, df = 18, $p < 0.005$). Each point is the mean of five individuals sampled from one acetone control or TCDD replicate. Open and closed circles represent acetone control and [^{3}H]TCDD groups, respectively.

possible that these and other unknown contaminants may have contributed to the developmental toxicity of TCDD in lake trout in the present study.

Species Differences in Sensitivity to TCDD Toxicity

Animal species vary greatly in their sensitivity to TCDD. The guinea pig is the most sensitive mammal with an LD_{50} of 1.0 part per billion (ppb) (1 μg/kg body weight; Schwetz et al. 1973), while the chicken embryo is the most sensitive avian species with an LD_{50} of less than 1.0 ppb (<1 ng/g egg; Higginbotham et al. 1968). Juvenile fish are relatively less sensitive to the lethal effects of TCDD with LD_{50}s in yellow perch (*Perca flavescens*), rainbow trout (*Oncorhynchus mykiss*), and

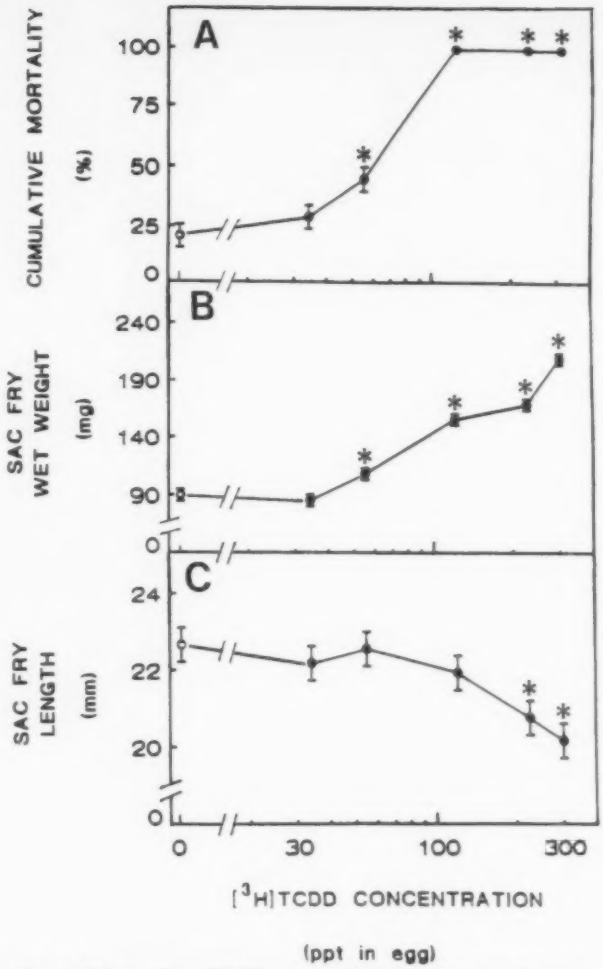

FIG. 6. Effects of egg TCDD concentration on (A) cumulative mortality at swim-up, (B) sac fry wet weight, and (C) sac fry length. Each point and associated vertical line is the mean ± SE of four replicates. Significant differences between control and TCDD groups are indicated by an asterisk ($p < 0.005$).

bluegill (*Lepomis macrochirus*) equal to 3, 10, and 16 ppb, respectively (3, 10, and 16 μg/kg body weight, respectively; Kleeman et al. 1988).

In general, early developmental stages are more sensitive to TCDD toxicity than adults. In rainbow trout, exposure of swim-up fry (21 d posthatch) to waterborne TCDD resulted in peak body burdens of 990 ppt and 45% mortality (Mehrle et al. 1988). In contrast, the LD_{50} for newly hatched rainbow trout sac fry, exposed as eggs to waterborne [^{3}H]TCDD, was 300 ppt (M. K. Walker and R. E. Peterson, unpubl. data). Thus, rainbow trout sac fry are 3 and 30 times more sensitive to the lethal effect of TCDD than rainbow trout swim-up fry (Mehrle et al. 1988) and juveniles (Kleeman et al. 1988), respectively.

When compared with other freshwater fish species, the early life stages of lake trout are among the most sensitive to TCDD. Newly hatched lake trout sac fry in the present study are five times more sensitive to TCDD (LD_{50} 65 ppt) than newly hatched rainbow trout sac fry (LD_{50} 300 ppt). Furthermore, when exposed as eggs, lake trout sac fry are more sensitive to the

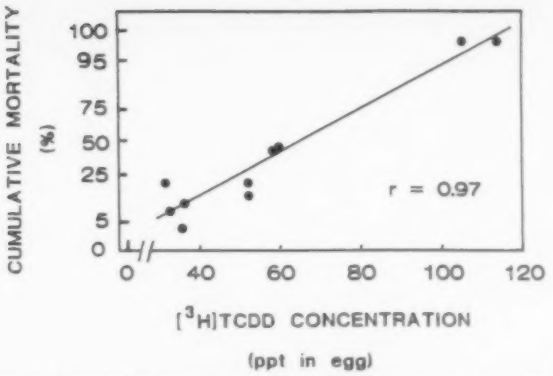

FIG. 7. Cumulative mortality of lake trout at swim-up as a function of the TCDD concentration in the egg. Cumulative mortality in TCDD groups has been corrected for mean cumulative mortality in the acetone control group (20.4%). Cumulative mortality is expressed on the ordinate on an angular transformation scale. Each point is the cumulative mortality for a single TCDD replicate.

lethal effects of TCDD than any mammalian, avian, or fish species investigated to date.

TCDD-Induced Mortality and Lesions during Lake Trout Early Development

For fertilized lake trout eggs containing 34–302 ppt TCDD, the greatest mortality occurred during the sac fry stage and was associated with subcutaneous edema of the yolk sac. TCDD-induced edema, quantified as an increase in sac fry wet weight, preceded and paralleled an egg TCDD concentration-related increase in sac fry cumulative mortality. Helder (1980, 1981) found similar results when rainbow trout and northern pike (*Esox lucius*) eggs were exposed to ppt concentrations of waterborne TCDD. TCDD-induced cumulative mortality of both rainbow trout and northern pike sac fry was closely related to the incidence of edema. Similar lesions and increased mortality have also been described in the Japanese medaka (*Oryzias latipes*) embryo following waterborne exposure of fertilized eggs to ppt concentrations of TCDD. In the Japanese medaka, TCDD-induced lesions developed prior to hatching and included pericardial edema, vascular hemorrhage, and collapse of the yolk sac, leading to mortality (Wisk and Cooper 1990).

The yolk sac edema seen in TCDD-exposed lake trout sac fry may have secondarily decreased body growth as reflected by shorter body length. Yolk sac edema appeared to reduce blood flow through the vitelline vasculature which could have secondarily decreased absorption of yolk nutrients and retarded growth (Spitsbergen et al. 1991). Rainbow trout and northern pike sac fry, exposed as eggs to TCDD, were also significantly shorter in length than controls (Helder 1980, 1981).

While the greatest TCDD-induced mortality occurred during the sac fry stage, a significant percentage of lake trout larvae (8–17%) died half-hatched in eggs containing the two highest concentrations of TCDD. Similarly, Helder (1980, 1981) observed half-hatching mortality in rainbow trout and northern pike, following exposure of eggs to TCDD.

Morphologically, TCDD-induced lesions are nearly identical to blue-sac disease (Spitsbergen et al. 1991), a naturally occurring syndrome in hatchery-raised salmonids (Wolf 1969; Roberts and Shepherd 1986). The development of both blue-sac disease and TCDD toxicity in lake trout consists of edema and hemorrhages that are sac fry stage specific; however, the etiology of blue-sac disease is poorly understood. A pathologic organism has recently been isolated from affected sac fry (Symula et al. 1990), but many exogenous factors can also induce the edema syndrome including reduced waterflow, increased water ammonia concentrations, and low dissolved oxygen levels (Burkhalter and Kaya 1977; Wolf 1969). The presence of ppt concentrations of TCDD in salmonid eggs can now be added to the list of factors that cause blue-sac disease.

Elimination of TCDD during Lake Trout Early Development

The persistence of TCDD in lake trout eggs and sac fry may contribute to its high toxic potency during early development. The absolute amount of TCDD remained constant in eggs and sac fry, but was rapidly eliminated from fry ($t_{1/2}$ = 35–37 d). Elimination of TCDD during lake trout early development is fry stage specific and in this context resembles the elimination of a PCB congener, 2,2′,5,5′-tetrachlorobiphenyl, during rainbow trout early development. Guiney et al. (1980) found this PCB congener to be very slowly eliminated from rainbow trout eggs and sac fry ($t_{1/2}$ = 231 d) but very rapidly eliminated from fry ($t_{1/2}$ = 15 d).

The lack of TCDD elimination during the egg and sac fry stages of lake trout probably results from a lack of TCDD metabolism; only the parent compound and no metabolites of TCDD were detected in extracts of eggs and sac fry. Furthermore, urinary, biliary, and fecal excretion do not occur during the egg and sac fry stages of development.

The reasons for the rapid elimination of TCDD from lake trout fry (post-swim-up) are not known. Lake trout fry were not analyzed for TCDD and TCDD metabolites; therefore, metabolism of TCDD and excretion of metabolites may be responsible for the rapid elimination of TCDD from fry. Juvenile rainbow trout have been shown to metabolize TCDD to more polar metabolites and excrete them in bile (Kleeman et al. 1986), and this may also occur in lake trout fry. However, fish have lower rates of xenobiotic metabolism compared with higher vertebrates (Hutzinger et al. 1972; Elcombe et al. 1979), and in higher vertebrates, TCDD is metabolized very slowly (Wroblewski and Olson 1985). Alternatively, the rapid elimination of TCDD from lake trout fry may be explained by the physiologic changes that occur during the developmental transition from sac fry to fry (swim-up). At swim-up, lake trout fry excrete bile and feces when exogenous feeding first begins, and the bile and feces may represent possible excretory routes for unmetabolized TCDD. In mammals, unmetabolized TCDD is directly excreted in the feces; this represents the major route of elimination of TCDD from the guinea pig (Olson 1986). In addition, as sac fry reach swim-up and yolk lipids are depleted, the lipid content of the whole organism rapidly declines. This decrease in total lipid content may cause the TCDD to redistribute out of the body and partition into the feces. Furthermore, feeding the TCDD-exposed fry a high-fat diet (Silver Cup® salmon starter, 14% crude fat by weight) may have accelerated this postulated redistribution; the dietary fat present in the gastrointestinal lumen of lake trout fry may have increased partitioning of TCDD into the feces and, subsequently, increased whole-body elimination of TCDD.

Significance to Lake Trout Early Life Stage Mortality in the Great Lakes

Field and laboratory studies have suggested that halogenated aromatic hydrocarbons in feral lake trout eggs are associated

with an increase in egg, sac fry, and/or fry mortality (Berlin et al. 1981; Mac et al. 1985; Mac 1988; Mac et al. 1988; Skea et al. 1986; Simonin 1990).

Toxicity Syndrome Characterized by Lake Trout Egg or Fry Mortality

Mac et al. (1985) found that the concentration of total PCBs and DDE in lake trout eggs from the Great Lakes was directly related to mortality of eggs and fry when monitored under hatchery conditions. Lake Michigan lake trout eggs had the highest concentrations of PCBs and DDE, followed by eggs from Lake Huron and Superior. Mortality of fertilized eggs from Lakes Superior, Huron, and Michigan equaled 4, 22, and 30%, respectively, while mortality of fry (from hatching to 139 d posthatch) equaled 41, 52, and 96%, respectively. Fry from Lake Michigan exhibited loss of equilibrium, erratic swimming behavior, and lethargy prior to death, characteristic of "swim-up" or "drop-out" syndrome. This behavior was not observed in fry that died from Lakes Huron or Superior.

In an earlier study, lake trout eggs collected from Lake Michigan were exposed after hatching as sac fry and fry to waterborne PCB, DDE, or the two in combination for 6 mo (Berlin et al. 1981). Cumulative mortality of fry was significantly higher than unexposed controls; however, fry mortality was not associated with a swim-up syndrome.

Recent evidence by Mac et al. (1988) directly correlated the concentration of a toxic PCB congener, 3,3′,4,4′-TetraCB, in Lake Michigan lake trout eggs with egg mortality; however, the egg concentration of this PCB congener was not correlated with fry mortality or with the observance of fry swim-up syndrome.

Toxicity Syndrome Characterized by Lake Trout Sac Fry Mortality and Blue-Sac Disease

Mortality in the above studies (Berlin et al. 1981; Mac et al. 1985, 1988) was not associated with blue-sac disease. In contrast, Simonin (1990) observed that lake trout eggs collected from Lake Ontario females exhibited a high incidence of blue-sac disease and associated mortality every year from 1977 to 1983, when egg collections stopped. In these studies, sac fry edema and mortality was female dependent, but was not correlated with concentrations of DDT, DDE, total PCBs, dieldrin, or mirex in the eggs.

Since adult lake trout from Lake Ontario have far greater concentrations of TCDD than lake trout from any of the other Great Lakes (Zacharewski et al. 1989; DeVault et al. 1989), it is possible that the blue-sac disease and mortality seen in lake trout sac fry collected from Lake Ontario may be caused by the presence of TCDD and other toxic halogenated aromatic hydrocarbons in the eggs. In support of this possibility, results of both the present study and a previous study from our laboratory (Spitsbergen et al. 1991) show that concentrations of TCDD in fertilized lake trout eggs as low as 40–55 ppt cause a significant increase in sac fry mortality that is associated with a blue-sac disease syndrome. However, Symula et al. (1990) found that when Lake Ontario lake trout eggs collected from the same females were incubated at 1.7–3.0°C, rather than 7–9°C, the incidence of blue-sac disease and mortality was significantly less, and they concluded that contaminants in the eggs were not responsible for the blue-sac disease and mortality.

In the Great Lakes, lake trout eggs are exposed to complex mixtures of contaminants such as mirex, toxaphene, dieldrin, DDE, DDT, PCBs, PCDFs, and PCDDs (Schmitt et al. 1985; Zacharewski et al. 1989). Until the ability of these contaminants (alone and/or in combination) to cause blue-sac disease is fully understood, the reason why halogenated aromatic hydrocarbon toxicity is associated with blue-sac disease in some lake trout studies but not others will remain unknown.

Our research shows that early life stages of lake trout are extremely sensitive when eggs are exposed to TCDD; however, the concentrations of TCDD and other toxic PCDD, PCDF, and PCB congeners in Great Lakes lake trout eggs are only beginning to be measured. Furthermore, in the environment, lake trout eggs are exposed to maternally derived PCDDs, PCDFs, and PCBs that are deposited during egg maturation, rather than to waterborne TCDD that is taken up across the chorionic membrane. In the Japanese medaka, maternally derived TCDD can cause embryotoxicity (Prince and Cooper 1990). Since exposure of lake trout eggs to maternally derived TCDD may influence the bioavailability, persistence, and lethal potency of TCDD in the developing embryo, future research will focus on the toxicity of maternally derived TCDD during lake trout early development.

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Discrimination between Atlantic Salmon (*Salmo salar*) of North American and European Origin using Restriction Analyses of Mitochondrial DNA[1]

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Twenty restriction endonucleases were used to study mitochondrial DNA (mtDNA) polymorphism in 11 hatchery strains of Atlantic salmon (*Salmo salar*) representing geographically separated populations in Europe and North America. The North American salmon mtDNAs studied were readily distinguished, by a minimum of seven restriction site differences, from fish of European origin. These results suggested that restriction analyses of mtDNA might provide a useful method for determining the proportions of European and North American Atlantic salmon caught in the West Greenland fishery. To test this proposition, we analyzed 328 salmon caught in the 1987 West Greenland fishery including 68 fish with coded wire or Carlin tags which provided the geographic source of the tagged salmon. We correctly identified the continent of origin for 67 of the 68 physically tagged salmon using two informative restriction endonucleases. This study provides a clear indication of the usefulness of mtDNA for discriminating between European and North American Atlantic salmon caught in the West Greenland fishery and for mixed-fishery analysis in general.

Vingt endonucléases de restriction ont été utilisées pour étudier le polymorphisme de l'ADN mitochondrial (ADNmt) chez 11 souches d'écloserie de saumon de l'Atlantique (*Salmo salar*) représentant des populations provenant de régions différentes, soit d'Europe et d'Amérique du Nord. Les ADNmt du saumon d'Amérique du Nord qui ont été étudiés se distinguaient facilement de ceux des espèces d'origine européenne par au moins sept différences de sites de restriction. Ces résultats indiquent que l'étude des sites de restriction de l'ADNmt pourrait constituer une méthode utile pour déterminer les proportions de saumons de l'Atlantique capturés dans la pêcherie de l'ouest du Groenland provenant d'Europe ou d'Amérique du Nord. Pour vérifier cette proposition, nous avons étudié 328 saumons capturés dans la pêcherie de l'ouest du Groenland en 1987, dont 68 pourvus de micromarques magnétisées codées ou d'étiquettes Carlin qui permettaient de déterminer leur provenance. En utilisant deux endonucléases de restriction informatives, nous avons identifié correctement le continent d'origine de 67 des 68 saumons marqués. La présente étude indique clairement que l'ADNmt est utile pour déterminer si le saumon de l'Atlantique capturé dans la pêcherie de l'ouest du Groenland provient d'Europe ou d'Amérique du Nord; cette méthode pourrait également convenir en général pour d'autres pêcheries.

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Commercial marine harvests of Atlantic salmon (*Salmo salar*) represent a classic problem in fisheries biology, namely that of managing a mixed-stock fishery. There is a major fishery for Atlantic salmon off the west coast of Greenland where the catch is composed almost entirely of North American and European origin one-sea-winter age salmon. The fish originate from both wild-run rivers and enhancement programs on both continents. For conservation and economic reasons it is important, on a year to year basis, to determine the relative contributions that different stocks of Atlantic salmon make to the West Greenland fishery. In fact, information on

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the composition and origin of the catch and estimates of the mortality rate based on these data are considered when yearly quotas are determined for the fishery. Thus the accuracy and timeliness of the data, particularly stock origin, are critical.

This paper provides information on levels of mitochondrial DNA (mtDNA) polymorphism within the Atlantic salmon and also demonstrates the utility of mtDNA as a genetic marker for distinguishing between fish of North American and European origin. Specifically, we assess restriction endonuclease analysis of mtDNA as a method for determining the proportions of European and North American Atlantic salmon caught in the West Greenland fishery. Thus our aim is identical to that of a number of other investigators who have used both genetic and nongenetic methods, with considerable success, to estimate the contribution of European and North American salmon to this fishery (see particularly Reddin 1986; Stahl 1987; Reddin et al. 1988; Verspoor 1988). Currently management advice concerning the compositon and origin of the salmon catch at West Greenland is based on scale ageing and meristics (Anonymous 1990). Problems associated with both the implementation and calibration of scale analyses for this fishery motivated the present study. This research also extends the findings of additional mtDNA surveys of anadromous and nonanadromous Atlantic salmon (Birt et al. 1986, 1991; Gyllensten and Wilson 1987; Bermingham et al. 1988; Hovey et al. 1989; Palva et al. 1989).

We first investigated 11 hatchery stocks of Atlantic salmon with historical origins in 10 different rivers in North America and Europe. We used restriction analyses of mtDNAs to characterize geographic population structure within Atlantic salmon and to determine whether or not mtDNA genotypic characters could provide qualitative markers useful for differentiating between salmon from North America and Europe. We next analyzed 328 Atlantic salmon caught in the 1987 West Greenland fishery. Using restriction analyses of mtDNAs, we determined the proportion of North American and European fish in the sample. Furthermore, we were later able to obtain coded wire or Carlin tag information for 68 of these salmon. By comparing data obtained from both the physical (coded wire or Carlin tags) and genetic (mtDNA) markers, we are able to evaluate the use of mtDNA analysis for determining continent of origin of harvested Atlantic salmon.

Materials and Methods

The Atlantic salmon included in this study are divided into two groups: 47 fish, representing 10 geographical stocks of Atlantic salmon (Connecticut River stocks were founded from Penobscot River fish), were collected from hatcheries and net pen facilities in the northwestern United States (Table 1). A second group of 328 fish caught in the Greenland fishery was collected at a fish processing plant in Nuuk, Greenland, in 1987. It should be noted that in the first group, small sample sizes coupled with possible loss of genetic diversity in hatchery populations (see Allendorf and Ryman 1987) suggest that only the most common mtDNA genotypes from the original populations were detected. In the second group, salmon were collected from a single processing plant over a short period of time, and thus, this sample should not be considered to represent the full geographic or temporal range of the West Greenland fishery. The coded wire and Carlin tagged salmon in the second group represent stocks that increase the geographic range of Atlantic salmon assayed (see Table 2) and diminish, but do not alleviate, sampling inadequacies associated with the hatchery group.

For the hatchery group, mtDNA was isolated in closed-circular form from fresh liver and/or heart if the fish was larger than 75 mm. Smaller fish (fry) were pooled and mtDNA was purified from fresh whole bodies homogenized after removal of the skins. Following isolation, mtDNAs were purified using procedures of cesium chloride/ethidium bromide gradient centrifugatin (Lansman et al. 1981). Purified mtDNAs were extracted with water-saturated butanol to remove ethidium bromide and dialyzed against TE (10 mM Tris, 1 mM EDTA, pH 7.5) to remove the cesium chloride. Aliquots of mtDNA were digested with 20 restriction enzymes per individual (or pooled sample) under the conditions recommended by the vendors (Bethesda Research Laboratories and Boehringer-Mannheim; see Table 1, footnote b, for listing of enzymes used). Resulting DNA fragments were end-labeled with appropriate [α-^{32}P]dXTP(s), sized by agarose gel electrophoresis (0.7–1.5%), and visualized by autoradiography (Brown 1983; Drouin 1980). The possibility of scoring two nonhomologous fragments as identical due to chance comigration was minimized by rerunning fragments of questionable identity side by side at different gel concentrations.

For the second group of 328 Atlantic salmon, crude genomic DNA was isolated from either liver or skeletal muscle samples that had been frozen on dry ice and stored at −80°C. (All steps in the DNA isolation procedure described below were carried out in 1.5-mL snap-top Eppendorf tubes.) About 100 mg of tissue from each fish was powdered in liquid nitrogen and incubated at 37°C, overnight, in a proteinase K/SDS solution (500 μL of STE (100 mM NaCl, 10 mM Tris, 25 mM EDTA, pH 7.5), 25 μL of a 10 mg/mL stock of proteinase K in STE, and 25 μL of 20% SDS). Following incubation the samples were extracted twice with an equal volume of PCI (25:24:1 mix of phenol, chloroform, and isoamyl alcohol) and twice with an equal volume of chloroform. The DNA in each sample was ethanol precipitated, pelleted, dried, and suspended in 250 μL of TE. Typical yields were about 25 μg, and approximately 1 μg of DNA from each individual fish was digested using the restriction enzymes *Dra* I and *Bst* EII. Additional aliquots from a subset of the 328 fish were digested with *Ava* II. DNA fragments were electrophoretically separated on 0.9% agarose gels (or 1.1% agarose gels for *Ava* II fragments), denatured, and transferred overnight onto Zetabind nylon filters. Following transfer the nylon filters were hybridized, for one to two nights, with ^{32}P random-primed or nick-translated Atlantic salmon mtDNA (probe mtDNA) which had been twice purified by ultracentrifugation. After washing the filters to remove the unincorporated probe mtDNA, restriction fragments were visualized by autoradiography.

A map of all restriction sites (with the exception of *Cla* I, *Stu* I, *Hind* II, and *Ava* II) was constructed using fragment sizes produced by single and double digestions of Atlantic salmon mtDNAs (Zehetner et al. 1987) (see Fig. 1). *Bam* HI, *Bcl* I, *Bgl* II, *Bst* EII, and *Xho* I restriction endonucleases each produce one or two cuts in Atlantic salmon mtDNAs and were easily mapped. Maps were considered complete when cleavage sites for a new enzyme could be assigned to locations internally consistent with those for the above enzymes. Position 0 of the approximately 16 800 base pair (bp) mtDNA of *S. salar* is an *Eco* RI site that we believe to be homologous with a conserved *Eco* RI site located at 7.5 kbp on Thomas et al. (1986) mtDNA maps of *Oncorhynchus* species. The proposed mitochondrial

TABLE 1. Sample identification numbers, composite mtDNA genotypes, and historical source of the hatchery populations used in this study.

Sample ID	N^a	Composite genotype[b]	Historical source of stock
O-99		CCCCCCCCCCCCCCCCCCCC	Connecticut River[d], CT, USA
O-100		CCCCCCCCCCCCCCCCCCCC	Connecticut River[d], CT, USA
O-97		CCCCCCCCCCCCCCCCCCCC	Penobscot River, ME, USA
O-98		CCCCCCCCCCCCCCCCCCCC	Penobscot River, ME, USA
O-95		CCCCCCCCCCCCCCCCCCCC	Union River, ME, USA
O-96		CCCCCCCCCCCCCCCCCCCC	Union River, ME, USA
O-142	3	CCCCCCCCCCCCCCCCCCCC	Grand Lakes, ME, USA
O-143	3	CCCCCCCCCCCCCCCCCCCC	Grand Lakes, ME, USA
O-195		CCCCCCCCCCCCCCCCCCCC	Grand Lakes, ME, USA
O-103		CCCCCCCCCCCCCCCCCCCC	St. Johns River, N.B., Canada
O-104		CCCCCCCCCCCCCCCCCCCC	St. Johns River, N.B., Canada
O-101		CCCCCCCCCCCCCCCCCCCC	Grand Cascopedia River, N.B., Canada
O-102		CCCCCCCCCCCCCCCCCCCC	Grand Cascopedia River, N.B., Canada
O-364		CCCDDDDCCCCCCCCCCCCX	Vogalax River, Iceland
O-365		CCCDDDDCCCCCCCCCCCCX	Vogalax River, Iceland
O-366		CCCDDDDCCCCCCCCCCCCX	Vogalax River, Iceland
O-173R		CCCDDDDCCCCCCCCCCCCX	Wester Ross River, Scotland
O-174R		CCCDDDDCCCCCCCCCCCCX	Wester Ross River, Scotland
O-175R		CCCDDDDCCCCCCCCCCCCX	Wester Ross River, Scotland
O-369		CCCDDDDCCCCCCCCCCCCX	Wester Ross River, Scotland
O-170		CCCDDDDCCCCCCCCCCCCX	Nanske River[e], Norway
O-134	5	CCCDDDDCCCCCCCCCCCCX/Y[c]	Morrum River, Sweden
O-137	5	CCCDDDDCCCCCCCCCCCCX/Y[c]	Morrum River, Sweden
O-138	4	CCCDDDDCCCCCCCCCCCCY	Neva River, Russia
O-139	4	CCCDDDDCCCCCCCCCCCCY	Neva River, Russia
O-140	4	CCCDDDDCCCCCCCCCCCCY	Neva River, Russia

[a]mtDNA was isolated from pooled samples where N is indicated; otherwise, mtDNA was isolated from a single individual.

[b]Letters, from left to right, refer to digestion profiles produced by the following restriction endonucleases: *Bam* HI, *Bcl* I, *Bgl* I, *Bgl* II, *Bst* EII, *Cla* I, *Dra* I, *Eco* RI, *Eco* RV, *Hind* III, *Hpa* I, *Pst* I, *Pvu* II, *Sac* I, *Stu* I, *Xba* I, *Xho* I, *Ava* I, *Hind* II, *Ava* II.

[c]The two pooled samples taken from Swedish salmon displayed all fragments characteristic of both the X and the Y *Ava* II restriction fragment profiles. This is most likely the result of pooling fish with different *Ava* II mtDNA genotypes.

[d]Derived from Penobscot River fish.

[e]Moni A/S commercial stock.

gene organization in Atlantic salmon is the same as that in human (Davidson et al. 1989b).

We estimate that the placement of cleavage sites on the Atlantic salmon map is accurate to within plus or minus several hundred base pairs. It is possible that we have failed to map a few restriction sites because they terminate small fragments or are coincident with other sites. The presence of one such site, which bounds an *Ava* I 500-bp fragment, was inferred during mapping. However, for most endonucleases the sizes of restriction fragments revealed by each enzyme totaled very close to 16.8 kbp, suggesting that we have observed most fragments. Comparing data from different laboratories, it is clear that large fragments cannot be sized accurately, and mapping provides valuable independent information on the true positions of distant sites (see Table 3).

Unmapped restriction sites (*Cla* I, *Stu* I, *Hind* II, and *Ava* II) were inferred from the fragment data, and presence/absence of both mapped and unmapped restriction sites was used to calculate the extent of sequence divergence (d) differentiating mtDNA haplotypes (Nei et al. 1985).

Results

Three distinct mtDNA genotypes were observed in the 47 hatchery group Atlantic salmon mtDNAs (representing both pooled and individual fish) surveyed with 20 restriction endonucleases (Table 1). These genotypes, or mtDNA haplotypes, are strongly patterned geographically. The North American salmon studied were readily distinguished from fish of European origin: the two mtDNA haplotypes from European fish differed at a minimum of seven restriction sites (*Bgl* II, *Bst* EII, *Cla* I, *Dra* I, and three or more *Ava* II sites) from the single mtDNA genotype observed in all North American Atlantic salmon (Fig. 1 and 2; Table 3). The minimum estimated mtDNA sequence divergence observed between the "North American" salmon mtDNA type and the "European" types is $d = 0.0072$.

The two mtDNA haplotypes obtained from European fish differ by only a single *Ava* II restriction site. The estimated sequence divergence between these two types is $d = 0.0011$. Again there is a geographic pattern to the distribution of the two mtDNA genotypes observed in European Atlantic salmon. Salmon from rivers in Iceland, Scotland, and Norway share a mtDNA halotype (referred to hereafter as the "European" type) that differs from the mtDNA haplotype from fish of Russian origin ("Baltic" type). The gain of an *Ava* II site in the mtDNAs of Baltic Sea fish relative to the mtDNAs of North Sea salmon was also observed by Gyllensten and Wilson (1987) in their study of Atlantic salmon from two Swedish rivers (Altran River,

TABLE 2. Geographic occurrence, in this and other studies, of the three mtDNA types defined in this report. Numbers in parentheses represent the coded wire and Carlin tagged Atlantic salmon collected in the West Greenland fishery.

River	"North American"	"European"	"Baltic"	Study[a]
North America				
Connecticut (ME, USA)	2			1
	(1)			
Penobscot (ME, USA)	2			1
	(37)			
Union (ME, USA)	2			1
Grand Lakes (ME, USA)	7			1
St. John (N.B., Canada)	2			1
Miramichi (N.B., Canada)	(5)			1
Grand Cascopedia (N.B., Canada)	2			1
Nepisiquit (N.B., Canada)	(1)			1
Kedgwick (N.B., Canada)	(1)			1
Tusket (N.S., Canada)	(1)			1
Medway (N.S., Canada)	(1)			1
North (N.S., Canada)	(1)			1
Five Mile Pond[b] (Nfld., Canada)	1			2
Exploits (Nfld., Canada)	1			2
Gambo[b] (Nfld., Canada)	29	5		3
Gambo (Nfld., Canada)	28	9		3
Total	124	14		
Europe				
Vogalax (Iceland)		3		1
Corrib (Ireland)		(3)		1
Lee (Ireland)		(3)		1
Erne (Ireland)		(1)		1
Shannon (Ireland)		(1)		1
Boyne (Ireland)		(1)		1
Wester Ross (Scotland)		4		1
Lussa (Scotland)		(1)		1
Tyne (England)		(4)		1
Ware (England)	(1)[c]	(3)		1
Itchin (England)		30	10	4
Mixed stock (France)		(2)		1
Nanske (Norway)		1		1
Atran (Sweden)		4		5
Total	1	61	10	
Europe, Baltic Sea				
Lule (Sweden)			5	5
Morrum (Sweden)		10[d]		1
Saimaa[b] (Finland)			17	6
Pielisjoki[b] (Finland)			6	6
Neva (Russia)			21	1, $N=12$; 6, $N=9$
Total			49	

[a]1, This study; Bermingham et al. (1988); 2, Birt et al. (1986); 3, Birt et al. (1991); 4, Hovey et al. (1989); 5, Gyllensten and Wilson (1987); 6, Palva et al. (1989).

[b]Nonanadromous stocks of Atlantic salmon.

[c]Only five of the physically tagged fish in this study were assayed with *Ava* II, but included in this group is the one fish with a "North American" haplotype tagged in the River Ware, England. None of the Newfoundland fish have been assayed with *Ava* II.

[d]These 10 fish were assayed as pooled samples and presumably include individuals with both the "European" and "Baltic" genotypes; see footnote c, Table 1.

North Sea; Lule River, Baltic Sea). In our study, both the "Baltic" and the "European" mtDNA genotypes were found in salmon from Sweden's Morrum River stock (Table 1; Fig. 2)

Two of the restriction endonucleases that produce genetic patterns useful for discriminating European from North American salmon, *Dra* I and *Bst* EII, were used to analyze genomic DNAs isolated from the 328 fish sampled from the west Greenland fishery. Seventy-four fish (23%) were identified as European and 254 (77%) as North American. Only one fish had a mixed European/North American genotype (a *Dra* I "North American" genotype and a *Bst* EII "European" genotype). Tissues from this fish were resampled and analyzed a second time with *Dra* I and *Bst* EII and for a first time with *Ava* II. *Ava* II and *Bst* EII yielded typical "European" mtDNA genotypes, but again, *Dra* I revealed the "North American" pattern. This is likely to represent the secondary loss of the *Dra* I site located at 4.25 kbp on our Atlantic salmon map in the mtDNA haplotype carried by this individual.

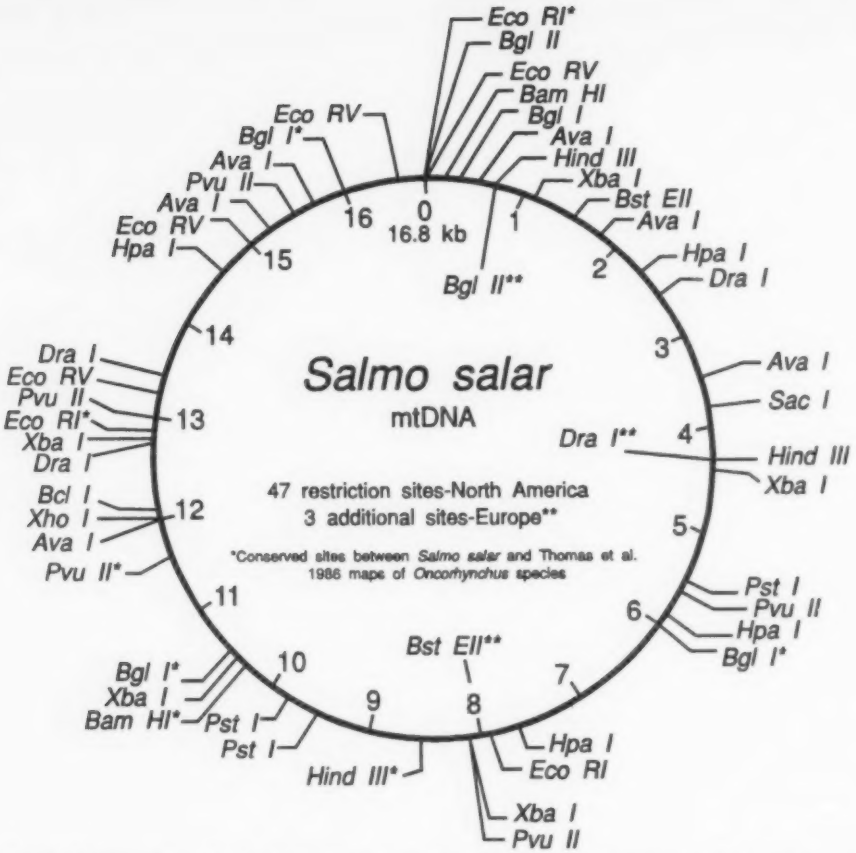

FIG. 1. Map positions of restriction endonuclease sites in the "North American" and "European" mtDNA genomes of Atlantic salmon. See text for details.

Of the 328 Atlantic salmon collected from the West Greenland fishery, physical tags indicating river, country, and continent of origin were recovered from 68 fish. Scoring the 68 marked salmon blind to the tag information revealed 47 North American salmon and 21 European salmon. Two fish had physical tag data and mtDNA genotype data that were not congruent. Resampling and digestion of the DNA with *Ava* II, *Bst* EII, and *Dra* I showed that laboratory error accounted for one of the misassignments; the new restriction patterns matched the tag identity. The other fish, which physical tag data identified as "European," was again characterized as "North American." This single true discrepancy between the genetic and physical tag data may have been due to error in tissue sampling or tag recording in the field, or the "North American" mtDNA genotype may occur in very low frequency in Europe. Nevertheless, the mtDNA data and the physical tag data agreed for 67 of the 68 Atlantic salmon tested from West Greenland.

The major feature of the mtDNA data in Atlantic salmon is the genetic divergence exhibited between North American and European forms. A secondary feature of the data is the genetic distinction between the "European" and "Baltic" mtDNA haplotypes. Figure 2, an autoradiograph showing the results of an *Ava* II digestion of both European and North American Atlantic salmon mtDNAs, depicts these genetic differences using one of the several informative enzymes. Although more detailed geographic sampling is required, the degree of concordance between physical tags and mtDNA genotype markers strongly suggests that mtDNA haplotypes may be used to assign continent of origin to individual Atlantic salmon with a high degree of confidence.

Discussion

Geographic patterns of mtDNA restriction site polymorphism have previously been described for a number of economically important fish species (Wilson et al. 1985, 1987; Kornfield and Bogdanowicz 1987; Grewe and Hebert 1988; Billington and Hebert 1988; Chapman 1989; Mulligan and Chapman 1989). The present study augments earlier surveys of Atlantic salmon using restriction enzyme analyses of mtDNA (Birt et al. 1986, 1991; Gyllensten and Wilson 1987; Hovey et al. 1989; Palva et al. 1989) and additionally provides a test analysis of stock composition in a mixed fishery off the West Greenland coast. The purposes of this research have been to (1) provide a data base on intraspecific mtDNA differentiation in Atlantic salmon over a wide geographic range and (2) assess the usefulness of restriction enzyme analyses of mtDNA for discriminating between Atlantic salmon of North American and European origin.

The level of mtDNA variation observed in Atlantic salmon is considerably lower than has been reported for several species of freshwater fishes (Bermingham and Avise 1986) but is sim-

TABLE 3. mtDNA fragment sizes observed in this and other published studies of Atlantic salmon. Only restriction endonucleases used in this study and revealing polymorphic mtDNA digestion patterns are listed. Fragments on one line are presumed to be homologous.

Enzyme	"North American"[a]	Newfoundland[b,c]		"European"[a]	England, Wales[d]		Sweden[e] (N. Sea)	Sweden[e] (Baltic)	Finland, Russia[f]	"Baltic"[a]
Bgl II	16 800	16 700	—	—		ND[g]	—	—	—	—
	—	—	15 800	16 050			15 600	15 600	14 700	16 050
	—	—	860	750			900	900	860	750
Bst EII	16 800	16 700	—	—		ND	ND	ND	—	—
	—	—	10 200	10 300					10 430	10 300
	—	—	6 500	6 500					6 160	6 500
Cla I	5 300		ND	—		ND	ND	ND	ND	—
	—			5 100						5 100
	3 850			3 850						3 850
	3 400			3 400						3 400
	[2 225][h]			[2 225]						[2 225]
	—			(200)[i]						(200)
Dra I	10 150	10 200	—	—		ND	ND	ND	ND	—
	—	—	8 500	8 450						8 450
	6 000	6 000	6 000	6 000						6 000
	—	—	1 700	1 700						1 700
	650	650	650	650						650
Pst I	12 500	—	13 300	12 500		ND	—	—	13 250	12 500
	—	10 300	—	—			10 350	10 350	—	—
	3 900	3 800	3 800	3 900			[3 900]	[3 900]	3 730	3 900
	—	3 100	—	—			—	—	—	—
	350	—	300	350			—	—	—	350
Ava II	—		ND	4 150	4 786	4 786	4 100	4 100	5 000	4 150
	2 525			2 525	2 951	2 951	2 350	2 350	2 500	2 525
	2 400			—	—	—	—	—	—	—
	2 250			2 250	[2 203]	[2 203]	2 100	2 100	2 200	2 250
	2 125			2 125	—	—	1 900	1 900	2 000	2 125
	1 825			—	—	—	—	—	—	—
	1 475			1 475	—	—	1 450	1 450	1 400	1 475
	—			1 375	1 396	1 396	1 340	1 340	1 300	1 375
	860			860	891	—	950	—	—	—
	815			—	—	—	—	—	—	—
	740			—	—	—	—	—	—	—
	550			550	582	582	600	600	[520]	550
	—			—	—	555	ND	ND	—	530
	415			415	414	414			380	415
	—			—	—	336			310	340
	—			[320]	322	322			300	[320]
	—			—	315	315			ND	—
	310			—	—	—				—
	235			235	211	211				235
	230			230	202	202				230
	—			145	143	143				145
	—			100	80	80				100

[a]This study; Bermingham et al. (1988).
[b]Birt et al. (1986, 1991).
[c]Davidson et al. (1989a).
[d]Hovey et al. (1989).
[e]Gyllensten and Wilson (1987).
[f]Palva et al. (1989).
[g]ND = no data.
[h]Square brackets = presumed doublet.
[i]Parentheses = fragment inferred, not actually seen on gel.

ilar to the amount of mtDNA restriction site polymorphism observed in many marine and diadromous fish species (Avise et al. 1986, 1987; Wilson et al. 1985, 1987; E. Bermingham and M. Shulman, unpubl. data). Nonetheless, there is an obvious geographic pattern to the distribution of mtDNA haplotypes observed in Atlantic salmon. It is the readily assayable mtDNA restriction site differences between the geographically separated groups of North American and European Atlantic salmon that make restriction analysis of mtDNA such a potentially powerful tool in the management of the West Greenland fishery. In addition, this result suggests that mtDNA may also be useful for analysis of other mixed fisheries involving anadromous species.

Both scale meristics and protein variation have been used to identify Atlantic salmon stocks (Reddin 1986; Stahl 1987; Reddin et al. 1988; Verspoor 1988). Scale samples used in the age

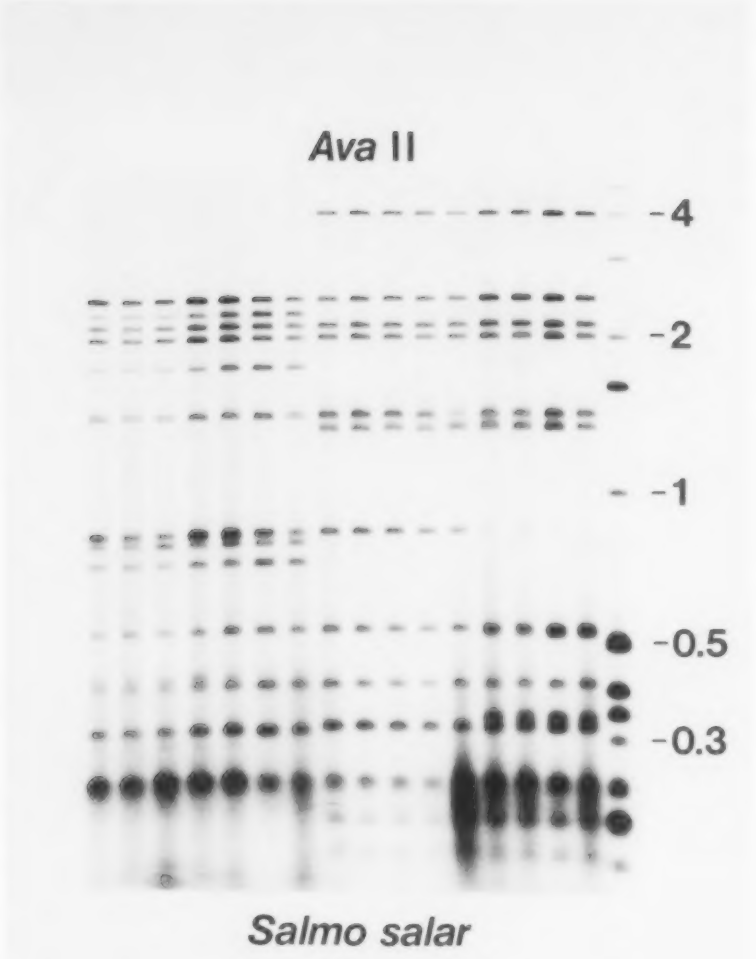

FIG. 2. Representative *Ava* II digests of mtDNAs isolated from Atlantic salmon. From left to right, the samples are O-99, O-100 (Connecticut River, USA); O-95R, O-96 (Union River, USA); O-103 (St. Johns River, Canada); O-101 (Grand Cascopedia River, Canada); O-143 (Grand Lakes, USA); O-364, O-365 (Vogalax River, Iceland); O-369, O-174R (Wester Ross River, Scotland); O-170 (Nanske River, Norway); O-134, O-137 (Morrum River, Sweden); O-138, O-140 (Neva River, USSR); molecular weight standard (BRL 1 kb ladder). mtDNAs were end-labeled and then size fractionated on a 1.5% agarose gel. (N.B. For total genomic DNA preps, however, separated on agarose gels, transferred to nylon filters, and hybridized to Atlantic salmon mtDNA, we typically are not able to resolve fragments smaller than 0.5 kb.) See Table 1 and text for comments on pooled samples.

analysis of salmon populations simultaneously provide a data source for continent assignments that is easy to collect and analyze. The ability to analyze numerous scale samples also ensures that the sampling design of the fishery is statistically robust. Regrettably, scale analysis has the disadvantage of being based on a character subject to annual variation. Variation in scale meristic characters is largely determined by environmental factors such as temperature, and thus, these characters are unlikely to be stable over time. A case in point was made by Reddin (1982) who demonstrated that scale circuli counts of the first-sea-year for European salmon decreased substantially between a 1968–70 database (Lear and Sandeman 1980) and a 1980 database (Reddin 1982). Use of the 1968–70 database in the analysis of scales from Atlantic salmon caught in the West Greenland fishery in recent years underestimated the proportion of European salmon caught there.

Currently, scale analysis is calibrated yearly by one of two methods. The first technique uses scale samples of two-sea-year salmon collected the following year to validate the previous year's scale analysis. The second method calibrates the scale analysis in the same year using an independent technique. Identifications in the same year have recently been undertaken with electrophoretic analyses of allozymes (Verspoor 1988). However, problems in implementing the allozyme analyses of Atlantic salmon to determine continent of origin resulted in data deficiencies in the assessment of the Greenland fishery. As reported by the ICES North Atlantic Salmon Working Group (Anonymous 1990), the inability to collect the required tissue samples and the inability to identify European genotypes using allozymes has left the scale meristics continent of origin analysis uncalibrated for annual variation since 1987. Clearly there is need for a technique to identify continent of origin of salmon that is more efficacious and has less rigorous sample collection requirements.

Restriction analysis of mtDNA has advantages compared with protein electrophoresis in determining the continent of origin of Atlantic salmon. First, the basic units of mtDNA analysis are distinct haplotypes in individual fish, in contrast with allozyme analyses which are typically based on population allele frequencies. In other words, mtDNA restriction fragment length polymorphisms (RFLPs) are genetic tags which can identify the continent of origin of individual fish, even in the absence of diagnostic, fixed differences in allozyme alleles between populations. In addition, mtDNA RFLPs share many of the attributes that have made physical tags so useful in fisheries management. They have the added benefit that all individuals carry a "tag" and thus are considerably more cost effective than physical tags. Furthermore, we report here the continent of origin of 328 salmon harvested in the 1987 Greenland fishery. Although the sample is too small and nonrandom to interpret trends in the fishery, it is large enough to illustrate the potential of scaling up this technique beyond the sample requirements of the annual calibration for the scale analysis.

The second advantage of mtDNA analysis over allozymes for mixed-fishery analysis concerns sample availability and preservation. The statistical power of population analyses based on allele frequencies is a function of the number of polymorphic protein loci that can be reliably scored. Maximizing the number of protein loci available for study in turn depends on the availability of several tissues (typically liver, muscle, and eye) and the adequate preservation of these tissues (samples frozen on dry ice or liquid nitrogen with subsequent storage at −70°C (Aebersold et al. 1987)). Both tissue collection and preservation can be problematic in remote areas. Also, the amount and source of tissues available are limited in species for which whole-fish market condition is important. As noted by Verspoor (1988), "In spite of the high classification success rates that are possible, protein variation has limited potential for use in the West Greenland fishery due to difficulties in obtaining samples of liver tissue necessary for determining protein genotypes." These problems are significantly reduced when nucleic acid methods are used. One hundred milligrams of tissue routinely yields sufficient high molecular weight DNA for 10–20 restriction enzyme digestions using either liver or skeletal muscle. In addition, tissue preservation is less critical in nucleic acid methods than in starch gel electrophoresis, which generally requires preservation of active enzymes. Although in the present study, tissues were collected on dry ice and maintained at −80°C, our laboratory routinely isolates high molecular weight DNAs and carries out mtDNA RFLP analyses from tissues preserved in 70–90% ethanol.

Although restriction enzyme analysis of mtDNA appears to be a valuable tool in the management of Atlantic salmon, caveats regarding these mtDNA analyses need to be discussed. The first is that our hatchery baseline sampling of Atlantic salmon mtDNA genomes, even with the addition of the physically tagged salmon collected in the West Greenland fishery, is not fully representative of the diversity and distribution of mtDNA haplotypes in the rivers of North America and Europe. This is particularly true in North America where all of our samples originated from a group of contiguous rivers in Maine and southern Canada. In fact, Birt et al. (1991) have recently observed what we have termed the "European" mtDNA haplotype in 20% of the anadromous and nonanadromous Atlantic salmon collected from the Gambo River in Newfoundland using restriction enzymes *Bst* EII and *Dra* I (Table 2). These are the same enzymes that we used to survey the 328 fish collected in the West Greenland fishery, and their data indicate that we may have underestimated the proportion of North American fish in that sample. Preliminary data, based on reasonable samples of salmon from only the Gambo and Penobscot rivers (Table 2), indicate that there may be a clinal distribution in North America of the "European" mtDNA haplotype and that it is completely replaced by the "North American" type in southern Canada and the United States. At the present time it is unknown whether or not *Ava* II will be able to distinguish betewen "European" mtDNAs of fish collected in North America and Europe. Only a single "North American" mtDNA haplotype has been observed (this study) in four independent surveys of wild and hatchery populations of European Atlantic salmon (this study; Gyllensten and Wilson 1987; Hovey et al. 1989; Palva et al. 1989) (Table 2).

Nevertheless, it is clear that a more complete geographic sampling of Atlantic salmon, especially in North America, is required. It is also clear that Atlantic salmon mtDNA genotypes need to be examined in greater detail. For example, by using restriction enzymes that cut at four or five base recognition sequences (see below) or directly sequencing portions of the mtDNA genome, it may be possible to find additional nucleic acid markers that unequivocally distinguish between fish of European and North American origin. A first step should be assays of Newfoundland and Quebec Atlantic salmon using the *Ava* II, *Hinf* I, and *Hae* III restriction enzymes that have already revealed informative mtDNA polymorphisms (Bermingham et al. 1988 and this study; Hovey et al. 1989; Palva et al. 1989).

Our observation that restriction sites may blink on and off in Atlantic salmon mtDNAs strongly suggests that salmon caught in the West Greenland fishery need to be tested with more than one restriction endonuclease. *Ava* II is a particularly useful enzyme for identifying salmon to continent of origin because it reveals multiple restriction site differences between "European" and "North American" mtDNA haplotypes. Thus, convergent mtDNA digestion profiles are highly unlikely with this enzyme. This is true for *Ava* II even though we typically cannot resolve mtDNA fragments smaller than 0.5 kbp using agarose gels and filter hybridization. To better appreciate the differences revealed by *Ava* II under conditions that would probably be used in a routine survey of the West Greenland fishery, imagine only the fragments larger than 0.5 kbp in Fig. 2 and Table 3.

A primary concern of managers of the West Greenland Atlantic salmon fishery is the determination of continent of ori-

gin of salmon harvested. However, there is also considerable interest among salmon biologists in being able to distinguish fish from different river systems. Recently published research by Palva et al. (1989) demonstrated that mtDNA markers can be used to discriminate between the geographically related Saimaa Lake and Neva River Atlantic salmon stocks used by the Finnish government in their breeding and stocking programs. Furthermore, a second group of investigators (Hovey et al. 1989) has even documented differences in the distribution of mtDNA haplotypes between Atlantic salmon spawning sites within a single river. Both of these studies are subject to the same criticism that can be leveled against our study: not enough fish have been sampled and temporal variation has not been surveyed. It remains to be seen if mtDNA analyses of Atlantic salmon will improve our knowledge of the regional genetic structure of Atlantic salmon populations beyond that which has resulted from allozyme studies (Stahl 1987; Verspoor 1988).

The northern rivers of North America and Europe have only been recolonized by Atlantic salmon following the last glaciation, within the last 8000 – 10 000 yr. Thus, not much time has elapsed for the accumulation of DNA base substitutions that are likely to distinguish between fish from geographically related drainages. Observed allozyme genotype differences in salmon populations are largely allele frequency shifts probably due to founder events and genetic drift (Stahl 1987; Verspoor 1988). It may be the case that in the absence of river stock specific mtDNA markers, allozymes representing unlinked protein coding loci or nuclear RFLPs are likely to provide better assays of local population subdivision. This is because the power of a test for population heterogeneity increases with the addition of unlinked polymorphic loci, and mtDNA is effectively a single linkage group. Nonetheless, mtDNA is a highly polymorphic locus with a large number of alleles in moderate frequency (e.g. six mtDNA haplotypes observed in fish collected from the River Itchen with the following frequencies: 0.565, 0.175, 0.135, 0.075, 0.025, and 0.025 (Hovey et al. 1989); four mtDNA haplotypes observed in nonanadromous salmon in the Gambo River (0.677, 0.177, 0.117, and 0.029); and two mtDNA haplotypes surveyed in anadromous salmon from the same river (0.757 and 0.243) (Birt et al. 1991)). If used in conjunction with allozymes or nuclear RFLPs, mtDNA may prove to be as useful for local Atlantic salmon stock differentiation as it appears to be for continent of origin determination.

This study and others cited herein provide convincing evidence that genetic stock identification of Atlantic salmon is clearly enhanced by restriction analyses of mtDNA. What is now required is a thoroughly representative geographic sampling of wild and hatchery stocks of Atlantic salmon surveyed for both informative mtDNA and allozyme characters. Only in this way will we know if the tools necessary for understanding the composition and origin of Atlantic salmon caught in the West Greenland fishery are in hand.

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Acoustic Measures of the Abundance and Size of Pelagic Planktivores in Lake Michigan[1,2]

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Based on acoustic data taken at night and vertically stratified by bottom depth (3–110 m only), the total number (±95% CI) of pelagic fishes in Lake Michigan was 43.4 ± 10.1 × 10^9 or 226.0 ± 55.2 kt in spring (mean density 0.7–3.8 fish·m^{-2} or 1.6–12.8 g·m^{-2}) and 115.8 ± 18.3 × 10^9 or 313.2 ± 74.3 kt in late summer, 1987 (mean density 1.1–7.9 fish·m^{-2} or 3.0–13.2 g·m^{-2}); approximately 30% of this increase in numbers (35% of biomass) occurred within Green Bay. Abundance estimates from horizontally stratified (by water column depth) data were within 9–11% of vertically stratified estimates during spring but over 20% higher during summer. By extrapolation to all water depths, we estimated total pelagic biomass as 274.6 kt for spring and 410.8 kt for summer. During both seasons, smaller fishes were nearer to the surface and nearer shore than larger individuals, and acoustic measures of size approximated the sizes of fishes caught in trawls. Bioenergetic model simulations suggest that 60% of the available production of alewife (*Alosa pseudoharengus*) was either consumed by stocked salmonines (52.9%) or commercially harvested (7.1%) in 1987. Underwater acoustics proved a valuable tool for lakewide assessments of fish abundances in the Great Lakes.

A partir de données acoustiques recueillies la nuit et stratifiées verticalement (selon la profondeur, de 3 à 110 m uniquement), on a estimé à 43,4 ± 10,1 × 10^9 ou 226,0 ± 55,2 kt le nombre total (IC de ±95%) de poissons pélagiques du lac Michigan au printemps (densité moyenne de 0,7 à 3,8 poissons·m^{-2} ou 1,6 à 12,8 g·m^{-2}) et à 115,8 ± 18,3 × 10^9 poissons ou 313,2 ± 74,3 kt à la fin de l'été, 1987 (densité moyenne de 1,1 à 7,9 poissons·m^{-2} ou 3,0 à 13,2 g·m^{-2}); environ 30 % de cette augmentation (35 % de la biomasse) s'est produite dans la baie Green. L'estimation de l'abondance à partir de données stratifiées horizontalement (selon la profondeur de la colonne d'eau) variait entre 9 et 11 % au printemps et était de plus de 20 % plus élevée en été. En extrapolant à toutes les profondeurs, nous avons estimé à 274,6 kt la biomasse pélagique totale au printemps et à 410,8 kt en été. Au cours de ces deux saisons, les poissons les plus petits se tenaient plus près de la surface et plus près de la rive que les gros, et la mesure acoustique de la grosseur correspondait à la taille réelle des poissons capturés à la palangre. Des simulations au moyen de modèles bioénergétiques indiquent que 60 % de la production disponible de gaspareaux (*Alosa pseudoharengus*) a été consommée par des populations de saumons (52,9 %) ou capturée à des fins commerciales (7,1 %) en 1987. L'acoustique sous-marine s'est révélée un outil précieux pour évaluer l'abondance du poisson dans toute l'étendue des Grands Lacs.

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Pelagic planktivores are the most abundant fishes in the Laurentian Great Lakes and play key roles in the trophic network and productivity of these systems (Carpenter et al. 1985, 1987; Kitchell et al. 1988; Hewett and Stewart 1989). Bloater (*Coregonus hoyi*), alewife (*Alosa pseudoharengus*), and rainbow smelt (*Osmerus mordax*) are the principal planktivores in Lake Michigan (Wells 1985; Brown et al. 1987). The recent collapse of alewife in Lake Michigan demonstrated that these planktivores may govern the size structure and species composition of the zooplankton community which can ultimately affect phytoplankton and water quality through cascading trophic interactions (Scavia et al. 1986, 1988; Jude

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[2]Contribution No. 759, National Fisheries Research Center Great Lakes, Ann Arbor, MI 48105, USA.

and Tesar 1985; Evans and Jude 1986; Eck and Wells 1987; McDonald et al. 1990). A major limitation to understanding how planktivores affect lower trophic levels is the absence of direct measures of planktivore abundances (Hewett and Stewart 1989; McQueen et al. 1989; Mazumder et al. 1990).

Pelagic planktivores also form the prey base for open-lake piscivores. In Lake Michigan, the predators are comprised of five species of salmon and trout, chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), rainbow trout (*O. mykiss*), lake trout (*Savelinus namaycush*), and brown trout (*Salmo trutta*), largely maintained through multiagency stocking programs. Despite the current predominance of bloaters in Lake Michigan, alewife and, secondarily, rainbow smelt continue to be the primary prey of salmon and trout (Jude et al. 1987; Stewart and Ibarra 1991). To determine the extent to which planktivore production limits piscivore production, a lakewide quantification of planktivore biomass combined with bioenergetic models of planktivore production and salmonine prey demand is required (Stewart et al. 1981; Lewis et al. 1987; Leach et al. 1987). Such quantitative assessment of trophic supply and demand has become increasingly recognized as an essential ingredient in fisheries management; but has only recently been applied in large systems (see review by Ney 1990).

Pelagic fishes are inherently difficult to sample with nets because they are distributed in three-dimensional space rather than two-dimensional space like benthic fishes. Problems of net avoidance and escapement are compounded by patchy spatial distributions that can change dielly, seasonally, or with the age of the fish and can be directly influenced by physical and biological processes (e.g. Brandt 1980; Brandt et al. 1980; Crowder et al. 1981; Crowder and Magnuson 1982; Rose and Leggett 1989, 1990). Patchy spatial–temporal distributions thus create a universal problem for assessing fish abundances, especially in large ecosystems.

Acoustic techniques provide a promising alternative to nets for sampling pelagic fishes because samples can be collected continuously throughout the water column to provide more complete information on how a species is distributed in time and space (Clay and Medwin 1977; Thorne 1983). The efficacy of sound travel in water has been exploited for over 40 yr to locate fishes, but recent technological and theoretical breakthroughs such as the deconvolution (Peterson et al. 1976; Ehrenberg et al. 1981; Clay 1983; Rudstam et al. 1987) and the multibeam techniques (Traynor and Ehrenberg 1979; Burczynski and Johnson 1986; Foote et al. 1986) have allowed echoes received from fish targets to be converted directly to estimates of *absolute* abundance and fish size.

We conducted a study (1986–89) to evaluate the feasibility of using underwater acoustics to measure planktivore abundances in Lake Michigan. In this paper, we derive lakewide acoustic measures of fish abundance and size during spring and summer 1987 using two different data stratification strategies. We then use data on abundance and bioenergetic models of growth rates to estimate lakewide production of alewife in Lake Michigan and to estimate the proportion of that production that is being withdrawn by commercial fisheries or eaten by stocked salmonines.

Methods

General Sampling Design

Acoustic surveys were conducted along 11 transects, distributed lakewide, during spring (20–30 May) and summer

FIG. 1. Bathymetric map of Lake Michigan showing approximate locations of acoustic transects.

(26 August – 10 September) 1987 to determine the numbers and biomass of pelagic fishes in Lake Michigan. Eight of the transects, located in the lake proper off Manistique, Sturgeon Bay, Port Washington, Waukegan, Benton Harbor, Saugatuck, Ludington, and Frankfort, were centered around bottom trawling transects used by the United States Fish and Wildlife Service (USFWS) to gather data for annual assessment of the forage base in Lake Michigan (Hatch et al. 1981). One of our other acoustic transects was in the lake proper off Two Rivers (included to obtain data from an area where a large-scale commercial fishery for alewife operated) and the other two were in Green Bay, one each in the upper and lower portions (Fig. 1).

During spring, all operations were from the University of Wisconsin R/V *Neeksay*. Acoustic data were taken continuously day and night along each transect. Bottom depths along the transect ranged from 3 m to at least 110 m (sometimes >160 m) in the lake proper. Temperature profiles (N = 123) were taken at various depths along each transect with a mechanical bathythermograph. Bottom trawls, each with a 7.6-m headrope and a 6-mm-mesh (bar measure) liner in the cod end, were towed both day and night at depths of approximately 10, 25, 50, 75, and 100 m (10 and 25 m only in Green Bay) to obtain data on fish sizes and species composition. A total of 77 tows was made, each lasting 10 min at a speed of approximately 1.5 $m \cdot s^{-1}$. Total lengths (millimetres) of 4924 (combined) alewife, rainbow smelt, and bloater were taken in the field to compare with lengths of fishes estimated acoustically.

Procedures in summer differed rather substantially from those in spring. The USFWS R/V *Cisco* and the Michigan Department of Natural Resources S/V *Steelhead* joined the R/V *Neeksay* in data collection. The transects at Manistique and Benton Harbor were acoustically surveyed only in daytime. Other acoustic sampling was the same as in spring, except for some changes in maximum depths sampled along transects in Lake Michigan proper; however, in no case was the maximum depth sampled less than 110 m in the lake proper. Temperature profiles (410 total) and bottom trawl samples (163) were obtained along each transect as in spring. In summer the trawling in the lake proper was conducted at depths of 9, 18, 22, 27, 31, 37, 46, 55, 73, 91, and 110 m during the day (R/V *Cisco*) and at night (S/V *Steelhead*) along each transect; the trawls each had a 11.9-m headrope and a 13-mm-mesh cod end and for each sampling effort were towed 10 min at a speed of 1.5 $m \cdot s^{-1}$ (Hatch et al. 1981). Bottom trawling in Green Bay in summer was carried out with the same gear and by the same procedure as in spring. Total lengths (millimetre) of 17 352 (combined) alewife, rainbow smelt, and bloater were measured to compare with lengths of fishes estimated acoustically.

Acoustic Sampling

We used a 120-kHz (Biosonics model 102) dual-beam (10°, 25°) echo sounder to measure fish abundances. The source level for the acoustic system was 211.6 dB re μPa at 1 m for spring and 215.4 dB re μPa at 1 m for summer. The overall system gains were −172.48 and −173.98 dB re V μPa for the 20 log R and 40 log R, respectively. The transducer beam pattern (b $(\Phi)^2$ was 0.0029282. The transducer was housed in a stable platform, aimed downward, and towed alongside the research vessel at a depth of 1–2 m from the surface at speeds of 2–3 $m \cdot s^{-1}$. Sampling rate was 48 $pulses \cdot min^{-1}$ and pulse length was 0.5 ms. Signals were adjusted for spreading loss by applying a 40 log R time-varied gain, digitized, and recorded on video cassettes. Reference voltages recorded on each cassette were used to calibrate signals during analyses.

The overall performance of the acoustic system was calibrated during spring and summer using either a standard ping-pong ball or a tungsten carbide reference sphere (Foote and MacLennan 1983). Reference targets were centered beneath the transducer at various depths (<10 m) and measured target strengths were compared with established values to adjust the system calibrations accordingly.

Acoustic data were processed by both echo-squared integration and dual-beam analyses. Echo-squared integration (echo processor, Powell and Stanton 1983) provides a measure of relative fish density that can be converted to absolute density using information derived from dual-beam processing and system parameters. Echo-squared integration values were corrected for the 40 log R by backcalculating from 40 log R to 20 log R amplification and averaged for each 1-m depth interval (beginning at 2.5 m below the transducer) for 120 s giving a horizontal resolution of approximately 240–360 m. Dual-beam analysis (Biosonics model 221 dual-beam processor) was used to determine measures of acoustic size (decibels) of fish targets (Burczynski and Johnson 1986; Burczynski et al. 1987). Acoustic size is the fraction of incident sound energy that is reflected by a fish back toward the transducer and is a function of the bearing of the fish in relation to the axis of the transducer signal. The dual-beam system uses two concentric transducers such that the two directivity functions are independent of the bearing angle and the ratio of the two directivity functions is monotonically increasing in bearing angle. Consequently, the ratio of the amplitude of two echo pulses uniquely determines the bearing angle. Mean target strengths were calculated for each stratum (see below) and were used to convert measures of echo-squared integration into measures of absolute fish density (i.e. number per unit volume).

Abundance and Size Estimation

Only data taken at night were used for abundance estimates, since most fishes migrated to the bottom during day and could not be assessed acoustically. To estimate lakewide abundances of planktivores, Lake Michigan was geographically stratified into regions centered around the acoustic transects (Hatch et al. 1981). Except for the area around Two Rivers, these regions were the same as those used by Hatch et al. (1981) for translating trawl catches into forage fish abundance. The Two Rivers region was delimited as half way from Two Rivers to Sturgeon Bay on the north and Port Washington on the south. Green Bay was divided into lower Green Bay, which extended from the mouth of the Fox River to a cross-bay line intersecting the center of Chamber Island, and upper Green Bay, which covered the rest of the bay. The lake and bay were then stratified by bottom depth based on depths of stations routinely bottom trawled. Bottom depth strata were 0–9, 10–18, 19–37, 38–55, 56–73, and 74–110 m. Fish densities at bottom depths less than 3 m (not sampled) were assumed to be the same as those in the adjacent 3–9 m depth stratum. Since data from depths greater than 110 m were incomplete, they were excluded from detailed statistical analyses. Mean fish densities per square metre of surface area (±95% confidence intervals based on echo-squared integration data) were calculated for each 2 min of sampling along the transect within each depth stratum; 2-min data sets had sufficiently low serial correlation (auto correlation coefficients <0.2) to justify this degree of lumping (see Williamson 1982; MacLennan and Mackenzie 1988). The average number of fish per square metre was then multiplied by the total area to estimate the total numerical abundances of fishes. We assumed that fish densities along each transect were representative of those in the entire region in which the transect was located.

A second method of data stratification (horizontal) was also used to examine the effect of stratification on lakewide abundance measures, given observed differences in fish distributions with bottom depth and depth in the water column. For each transect, the acoustic data along each transect were horizontally stratified by water column depths of 4–9, 10–18, 19–37, 38–55, 56–73, and 74–110 m. Average fish densities per unit volume (±95% confidence intervals) were calculated from the 2-min data sets in each depth stratum. Total fish abundances were obtained by multiplying by lake volumes.

Conversion of fish numbers to biomass required two sets of calculations. First, measured target strengths (decibels) of fishes for each stratum were converted to fish lengths using Love's (1971) empirical relation between target strength (TS, decibels) and fish total length (L, centimetres) for data obtained with the 120-kHz system; $TS = 19.1 \log (L) - 63.85$. Then, fish lengths ($L$, millimetres) were converted to weight (W, grams) by the nonlinear regression $W = 0.00000117\, L^{3.35868}$. In computing the length–weight equation, we assumed that the relative numbers of bloater, alewife, and rainbow smelt in our acoustic samples were the same as in our bottom trawl samples and

derived the equation from the combined length and weight measurements taken from the three species. (N = 1079, R^2 = 0.97) caught in the bottom trawls. Absolute fish biomasses were then calculated by multiplying mean fish weight (grams) by the total number of fishes in each stratum.

Alewife Production and Harvest

We used the summer 1987 estimate of lakewide fish biomass to calculate annual alewife production and the proportion of that production that was either consumed by stocked trout and salmon or withdrawn by the commercial fishery. The alewife proportion of total biomass was estimated as the proportion of alewife biomass collected in bottom trawls during the day. We used the bioenergetics model (Stewart and Binkowski 1986; Hewett and Johnson 1987) and parameters derived for Lake Michigan alewife by Hewett and Stewart (1989). For calculation of age-specific annual production, the lakewide biomass estimate for summer was assumed to be the biomass existing on 30 August. We assumed that all accumulated gross production of alewife was available for salmonine consumption except for production among larvae that did not survive to the juvenile stage, and thus were never vulnerable to predation by salmonines. This assumption allowed for a maximum estimate of alewife production that would be available to salmonine predation because some alewife, particularly in their first year, occupy habitats (e.g. the epilimnion) that are not frequented by salmonines. Salmonine predation rates for 1987 were estimated from bioenergetics modelling simulations developed by Stewart and Ibarra (1991). In estimating the rates, we did not include estimates for those lake trout stocked on offshore deep reefs, since they feed mainly on bloaters and deepwater sculpins (M. Miller, Wisconsin Department of Natural Resources, Madison, WI, pers. comm.).

Results

Fish Distributions and Water Temperature

Spring

During spring, thermal stratification of water in the northern half of Lake Michigan was weak, with surface temperatures ranging from 4.2 to 10.3°C (Fig. 2). In the southern half, particularly in the extreme southeastern area, thermal stratification was somewhat more pronounced, and surface waters were generally warmer (8.5–16.5°C); the thermal gradient off Saugatuck extended from approximately 9 to 36 m. Surface waters in the western regions of the lake were 2–4° cooler (when bottom depth was 50 m) than in eastern regions of corresponding latitude. Surface water temperatures in Green Bay ranged from 7.5 to 11.0°C and little stratification was evident.

In general, acoustic scatterers were uniformly distributed in the bottom 10–30 m of the water column (Fig. 3), particularly in those areas dominated by bloater. Fish densities generally declined in water over 100 m deep. In areas of weak stratification, we observed some midwater scatterers during the day, but most fishes were near bottom during the day.

Based on bottom trawl catches, species composition differed considerably according to geographic areas of the lake (Fig. 4). Alewife composed the largest proportion (numerically) of the fish community on the western shore (71% in Sturgeon Bay, 88% in Two Rivers, and 46% in Port Washington). The largest catches of alewife occurred at a depth of 50 m. The largest catches of alewife for all depths combined were off Two Rivers (46.6% of the lakewide totals). Bloater dominated the catches on the eastern shore. With a single exception (10 m, Ludington), numbers of bloater in the catches made up at least 73% (as much as 95%) of the total. Rainbow smelt were most numerous in the catches in Green Bay, making up 64% of the totals (depths combined) in the south and 73% in the north. On a lakewide basis (excluding Two Rivers), alewife made up 13%, bloater 74%, and rainbow smelt 13% of the total numbers of fishes caught.

Summer

Surface temperatures during summer usually ranged from 18.0 to 20.9°C and the thermocline was more pronounced than in spring (Fig. 2). Offshore, the thermocline depth ranged from 13 to 25 m and generally intersected the bottom nearshore at depths between 18 and 35 m. As a result of upwelling during our sampling off Two Rivers and in shallower areas off Sturgeon Bay, we recorded lower surface water temperatures (15.9–17.9°) in those areas than in others. Water temperatures in Green Bay ranged from 19.9 to 20.4°C at the surface and never fell below 7.2°C in water less than 50 m deep.

Acoustic scatterers were strongly concentrated in the broad region where the thermocline intersected the bottom, but scattering layers also appeared in warmer waters within the top half of the thermocline (e.g. compare Fig. 2 and 3 (bottom panels)).

Acoustic scattering was distinctly different during day and night in both spring and summer. During the day, the scattering was patchier because fishes were aggregated (Brandt 1989). At night, acoustic scattering was more uniform because fishes were dispersed. Night abundance estimates were higher because nocturnal vertical migrations brought more fishes into the detection range of the acoustical equipment. Diel studies showed that alewife and adult rainbow smelt were generally strong vertical migrators that were near bottom during the day and moved to middle or upper levels of the water column at night (Brandt 1989). On average, less than 1% of alewife and 2% of rainbow smelt were available to bottom trawls at night. Catch per unit effort (CPUE) of adult bloater on the bottom at night was about 14% of that during the day, indicating that this species also migrates vertically.

Bottom trawl catches showed that fish geographic distributions were different in summer than in spring. In summer, alewife were more evenly distributed across the lake and did not dominate the catches in any region (Fig. 4), rainbow smelt predominated in the catches off Manistique, making up 78% of the total numbers caught, and bloater dominated the catches in all other areas composing 54.3–87.5% of the totals. Bloater were generally concentrated at temperatures near 8°C. Lakewide, alewife made up 7%, bloater 70%, and rainbow smelt 23% of the total numbers of fishes caught. Alewife made up 14%, bloater 78%, and rainbow smelt 8% of the area-weighted biomass.

Size of Targets

Spring

During spring, smaller fishes were generally higher in the water column (Table 1) and where bottom depths were shallower (Table 2) than were larger fishes. Mean lengths of fishes ranged from 53 to 107 mm in the upper 37 m of the water column and from 132 to 156 mm in the 74–110 m stratum. Mean fish lengths at bottom depths less than 37 m (data from all strata combined) were generally between 60 and 90 mm (73–

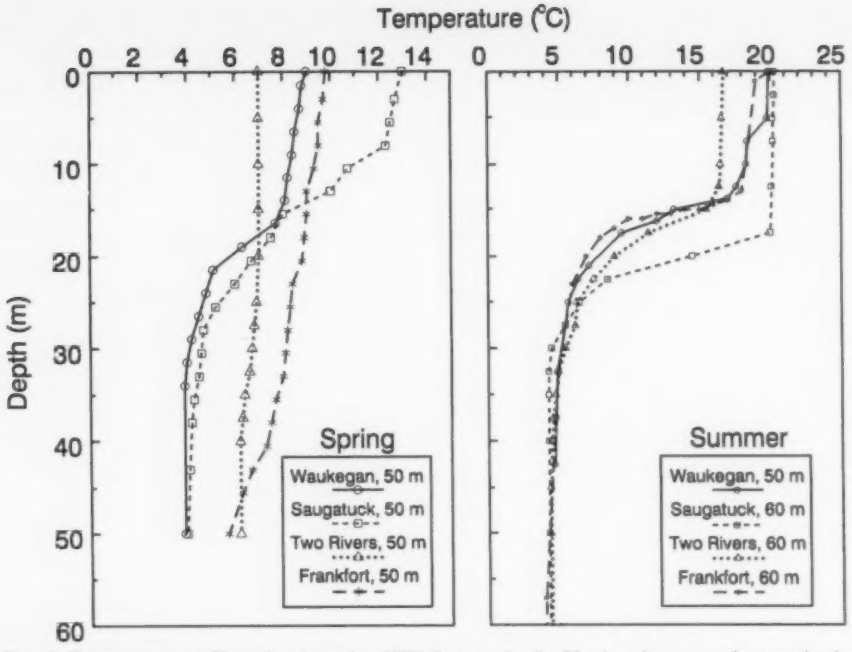

FIG. 2. Temperature profiles taken in spring 1987 (bottom depths 50 m) and summer (bottom depths 50 or 60 m) off four regions of Lake Michigan.

127 mm in the northwestern regions off Sturgeon Bay, Two Rivers, and Port Washington) whereas at depths greater than 73 m, mean lengths were 109–132 mm.

Fishes caught in bottom trawls were mostly small. On a lakewide basis, alewife were composed mainly of yearlings that generally were 65–100 mm long ($\bar{x}$ = 87 mm, N = 1333). Bloater were mainly 80–90 mm long, although a few were more than 200 mm long ($\bar{x}$ = 112 mm, N = 2820). Rainbow smelt were numerically dominated by small individuals 50–80 mm long ($\bar{x}$ = 74 mm, N = 771).

Acoustic estimates of the size of fishes in the water column at night were similar to sizes of fishes caught during the day in bottom trawls (compare Tables 1 and 2 with Fig. 5). For a more specific example, we show the comparison of the length–frequency distribution of fishes caught in bottom trawls during the day off Ludington with the acoustic measures of fish size at night. Mean lengths of fishes caught in bottom trawls during the day were 94 mm at depths of 10 and 29 m (Fig. 6) whereas mean fish lengths estimated acoustically at night were 66 mm in the 10–18 m stratum and 90 mm in the 19–37 m stratum. Acoustic data taken during the day off Ludington showed that mean fish length in the entire water column was approximately 71 mm, suggesting that the smallest fishes do not migrate to the bottom during the day; hence, we would expect estimates of fish sizes derived from bottom trawls to be somewhat larger than those derived from acoustics. Mean length of fishes (162 mm) caught in a bottom trawl at 75 m during daytime was similar to the mean length of fishes (156 mm) assessed acoustically within the 74–110 m water column depth stratum at night. It would not be valid to compare sizes of fishes caught in trawls with sizes of fishes estimated in the water column on finer spatial or bathymetric scales because the degree of inshore–offshore movements in concert with diel vertical migrations is not known.

Summer

In summer, as in spring, smaller fishes were generally distributed in shallower areas than were larger fishes. Mean fish lengths were always more than 100 mm in the 56–110 m strata of the water column but were usually less than 70 mm in the 0–9 and 10–18 m strata (Table 1). Mean fish lengths were generally between 50 and 90 mm at bottom depths less than 37 m (except at Port Washington where they ranged from 94 to 102 mm) whereas mean fish lengths were generally greater than 90 mm at bottom depths greater than 56 m (Table 2).

Some regional differences in fish sizes were apparent. At bottom depths greater than 56 m, fish lengths (97–129 mm) were generally larger in western Lake Michigan than fish lengths (75–95 mm) in eastern Lake Michigan (Table 2). The smallest fishes (mean size of 49 mm) were found in the shallow water of Green Bay.

Fishes caught in bottom trawls in summer were generally larger than those caught in spring (Fig. 5). On a lakewide basis, the rainbow smelt had a trimodal size–frequency distribution with the smallest mode ranging from 35 to 55 mm and the largest mode extending from 130 to 150 mm. Bloater were most abundant at lengths of 95–125 mm, but good numbers were 125–175 mm and lengths ranged from 60 to over 250 mm. Alewife ranged from less than 40 to over 200 mm long with a mode at about 150–185 mm. Comparisons between the size–frequency distributions from spring and summer showed that young-of-the-year bloater and yearling alewife were not well represented in the summer bottom trawl catches. Also, bottom trawling in summer (due to the larger net) probably took some larger fishes missed by spring trawling.

As in spring, acoustic estimates in summer of sizes of fishes in the water column at night compared favorably with sizes of fishes caught during the day in bottom trawls. For example, we compared the length–frequency distribution of fishes caught in bottom trawls during the day off Ludington with the acoustic

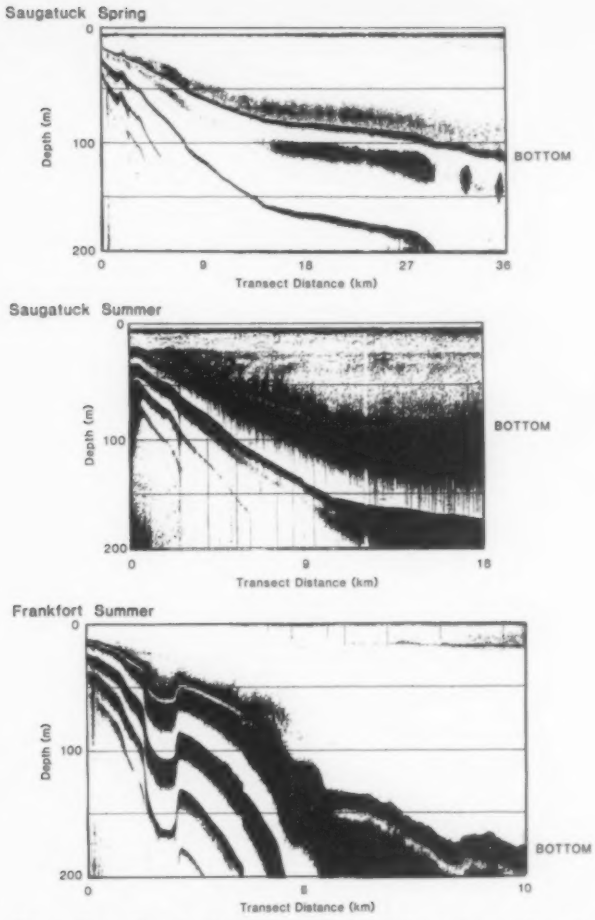

FIG. 3. Examples of echograms of fish scattering patterns taken off Saugatuck on 27 May (upper panel) and 6 September (middle panel) and off Frankfort on 1 September (bottom panel). Scattering is not corrected for sampling volume. Horizontal lines are at depth intervals of 50 m.

estimates of lengths of fishes in the water column at night. Lengths of fishes caught in bottom trawls off Ludington steadily increased with bottom depth from a low of 51 mm at 9 m to a high of 189 mm at 91 m (Fig. 6). This was mostly due to a shift in species composition from 99.5% rainbow smelt at 9 m, to 47.4% rainbow smelt and 52.2% bloater at 27 m, to 5.4% rainbow smelt and 94.0% bloater at 55 m, to 67.6% bloater and 31.5% alewife at 91 m. Mean fish lengths estimated acoustically at night ranged from 61 to 70 mm in water shallower than 37 m and were progressively larger in deeper water (Tables 1 and 2).

Fish Numerical Abundances in Spring

Fish densities per unit surface area in spring varied with bottom depth and region. Highest densities in every region of the lake proper occurred where bottom depths were less than 56 m (Table 3). The two highest densities, 7.23 fish·m^{-2} (Sturgeon Bay) and 5.84 fish·m^{-2} (Waukegan), were recorded where bottom depths were 19–37 m. Densities generally declined to less than 1 fish·m^{-2} where water depths exceeded 56 m. Fish densities in Green Bay were more uniform according to bottom depths, ranging from 0.56 to 1.69 fish·m^{-2}. Regional averages of fish densities (data from all depths combined) ranged from 0.72 fish·m^{-2} at Manistique to 3.76 fish·m^{-2} at Sturgeon Bay (Table 4). If each transect is considered an independent random measure of fish density, then the overall mean fish density (unweighted by area) was 1.39 fish·m^{-2} for the lake proper and 1.15 fish·m^{-2} for Green Bay.

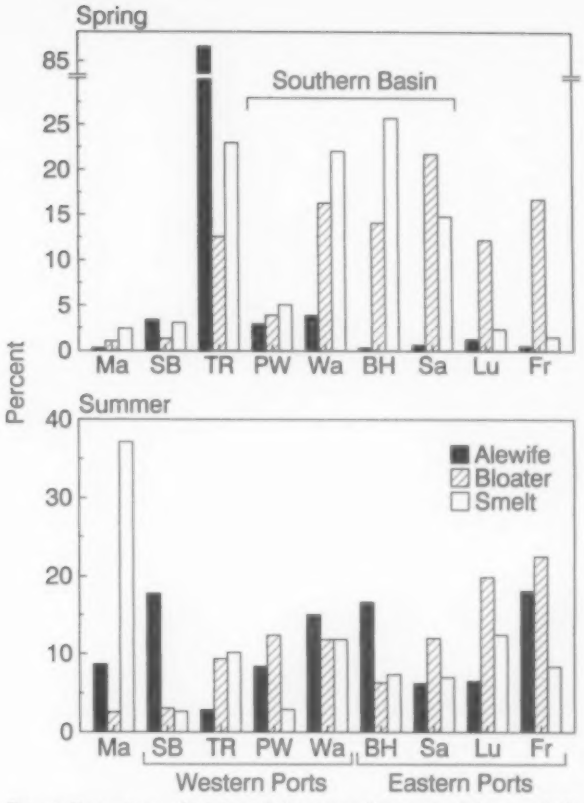

FIG. 4. Percentage of total catch by region for each species caught in bottom trawls in Lake Michigan proper during the day for spring and summer 1987. Region abbreviations: Ma, Manistique; SB, Sturgeon Bay; TR, Two Rivers; PW, Port Washington; WA, Waukegan; BH, Benton Harbor; Sa, Saugatuck; Lu, Ludington; Fr, Frankfort.

Fish densities per unit volume in spring ranged from 0.0002 to 0.1965 fish·m^{-3} (Table 5). Highest densities of fishes per unit volume within the lake proper were found in the uppermost stratum (0–9 m) at all locations except Frankfort where peak densities were at intermediate levels. The concentration of fishes in the 38–55 m stratum at Frankfort was associated with a layer of fishes extending offshore from the steep dropoff in bottom (Fig. 3). Fish densities were generally lowest in the deeper (>56 m) parts of the water column. The highest density of fishes per unit volume was in the uppermost stratum off Sturgeon Bay, where an upwelling in progress during our sampling may have forced fishes to move close to the surface.

Total numbers of fishes within the 0–110 m depth range of Lake Michigan during spring 1987 were estimated at about $43.4 \pm 10.1 \times 10^9$ and $47.3 \pm 9.5 \times 10^9$ using bottom depth (vertical, Table 6) and water column (horizontal) stratification, respectively. We estimated that 5.0–10.2% of these fishes were in Green Bay. Confidence intervals by region ranged from 8.0

TABLE 1. Average total length (mm) and weight (g) of fishes at different depths in the water column at night during spring and summer 1987. Fish lengths (TL) were estimated acoustically and converted to fish weight ($W = 0.00000117\ L^{3.35868}$). Sample size per measurement ranged from 12 to 4459 (median 339, quartiles 125, 624).

	Water column depth (m)											
	0–9		10–18		19–37		38–55		56–73		74–100	
Region	mm	g	mm	g	mm	g	mm	g	mm	g	mm	g
					Spring							
Sturgeon Bay	89	4.1	80	2.9	98	5.6	123	12.1	124	12.6	152	25.0
Two Rivers	106	7.4	53	0.7	91	4.4	103	6.8	122	11.9	143	20.4
Port Washington	107	7.7	76	2.4	62	1.2	94	5.0	117	10.2	132	15.4
Waukegan	82	3.2	55	0.8	56	0.9	76	2.4	101	6.3	139	18.5
Benton Harbor	60	1.1	73	2.1	93	4.8	96	5.3	124	12.5	140	19.0
Saugatuck	63	1.3	74	2.3	86	3.7	81	3.0	108	7.8	139	18.6
Ludington	70	1.9	89	4.2	82	3.1	94	5.0	119	10.9	156	27.3
Frankfort	55	0.8	67	1.6	76	2.4	95	5.2	113	9.3	140	18.8
Manistique	68	1.7	80	2.9	87	3.8	106	7.4	128	14.0	145	21.3
Green Bay (upper)	98	5.7	79	2.8	85	3.5	—	—	—	—	—	—
Green Bay (lower)	71	1.9	60	1.1	89	4.1	127	13.5	—	—	—	—
					Summer							
Sturgeon Bay	67[a]	1.6	64[a]	1.4	80	2.8	116	10.0	134	16.5	145	21.5
Two Rivers	67	1.6	64	1.4	98	5.6	114	9.5	149	23.5	161	30.0
Port Washington	108	7.9	119	11.1	87	3.8	130	14.6	135	16.9	127	13.5
Waukegan	91	4.5	74	2.2	78	2.6	93	4.8	117	10.5	128	14.0
Saugatuck	60	1.1	39	0.2	52	0.7	88	4.0	105	7.1	118	10.7
Ludington	66	1.5	61	1.1	70	1.8	120	11.1	137	17.6	135	16.7
Frankfort	51	0.7	56	0.8	63	1.3	96	5.4	123	12.4	130	14.7
Green Bay	46	0.4	95	5.1	102	6.5	95	1.2	—	—	—	—

[a]Derived from analyses of the data off Two Rivers.

to 34.5% of the mean if the lake was stratified by bottom depth and from 10.8 to 38.1% if the lake was stratified by water column depth.

Fish Biomass in Spring

Total fish biomass was estimated to be 226.0 ± 55.2 kt (Table 6) and 201.7 ± 38.7 kt using vertical and horizontal stratification, respectively. We obtained these values by multiplying the mean weight of fishes by their total estimated numbers in each vertical or horizontal stratum (Tables 1 and 2) in Lake Michigan in spring, where bottom depths were 0–110 m. Fishes in Green Bay contributed an estimated 4.7–5.3% of the total biomass. Confidence intervals by region ranged from 13.5 to 44.5% of the mean when the lake was stratified by bottom depth and from 7.9 to 39.5% when the lake was stratified by water column depth. Average biomass in the various regions ranged from 1.6 to 12.8 $g \cdot m^{-2}$ (Table 4). Biomass was highest in northwestern Lake Michigan off Two Rivers and Sturgeon Bay and lowest in lower Green Bay and off Manistique in the northernmost portion of the lake.

Fish Numerical Abundances in Summer

The number of fishes per unit surface area varied with depth and region in summer as in spring (Table 3). Fish densities per unit surface area (in summer) were highest where bottom depths were 10–55 m except off Sturgeon Bay and in lower and upper Green Bay where they were densest where bottom depths were 0–9 m (Table 3). Fish densities per unit area were generally lowest where bottom depths were 74–110 m. Highest fish densities occurred within the 0–9 m stratum near the mouth of Green Bay. These fishes were mostly small individuals (Table 2). Regional average number of fishes per unit surface area ranged from 1.11 fish·m^{-2} at Two Rivers to 5.32 fish·m^{-2} and 7.91 fish·m^{-2} in Green Bay (Table 4). The highest densities in the lake proper were in the northern ports at Sturgeon Bay (3.30 fish·m^{-2}) and Frankfort (4.01 fish·m^{-2}). The unweighted (by area) mean fish density was 2.48 fish·m^{-2} for the lake proper and 6.62 fish·m^{-2} for Green Bay. These densities were 78 and 476% higher than during spring. Fish densities per unit volume ranged from 0.0002 to 1.15 fish·m^{-3} (Table 5). Fishes were densest in the epilimnion where they were primarily young-of-the-year, particularly in Green Bay.

Total numbers of fishes within the 0–110 m depth range during summer 1987 were estimated at 115.8 ± 18.3 × 10^9 using stratification by bottom depth (Table 6) and 167.0 ± 23.5 × 10^9 using stratification by water column depth. The value for stratification by bottom depth represented a 2.7-fold increase over spring. An estimated 19.7–22.6% of all fishes were located in Green Bay, and of the total numbers of "new" fishes from spring to summer, about 30% came from Green Bay. Confidence intervals by region ranged from 7.1 to 22.4% of the mean when the lake was stratified by bottom depth and from 11.3 to 21.8% of the mean when it was stratified by water column depth.

Fish Biomass in Summer

Total fish biomass in summer where bottom depths were 0–110 m was 313.2 ± 74.3 and 386.0 ± 49.7 kt using bottom

TABLE 2. Average total length (mm) and weight (g) of fishes in the water column at night during spring and summer 1987. Fish lengths (TL) were estimated acoustically and converted to fish weight ($W = 0.00000117\ L^{3.35868}$). Sample size per measurement ranged from 22 to 4337 (median 380, quartiles 124, 725).

	Bottom depth (m)											
	0–9		10–18		19–37		38–55		56–73		74–100	
Region	mm	g	mm	g	mm	g	mm	g	mm	g	mm	g
					Spring							
Sturgeon Bay	96[a]	5.2	96	5.2	77	2.6	123	11.9	128	13.8	132	15.6
Two Rivers	95	7.5	104	10.2	91	6.5	112	13.0	94	7.2	109	11.8
Port Washington	127[a]	13.6	127	13.6	73	2.1	89	4.2	91	4.5	115	9.6
Waukegan	65	1.4	76	2.5	70	1.8	74	2.2	97	5.5	113	9.1
Benton Harbor	66[a]	1.5	66	1.5	93	4.9	94	4.9	119	10.9	132	15.5
Saugatuck	59[a]	1.0	59	1.0	84	3.4	94	4.9	103	6.8	113	9.2
Ludington	66[a]	1.5	66	1.5	90	4.3	88	3.9	109	8.2	124	12.7
Frankfort	75[b]	2.3	75[b]	2.3	75	2.3	90	4.2	102	6.6	125	12.9
Manistique	84[a]	3.4	84	3.4	86	3.7	101	6.4	127	13.6	119	11.0
Green Bay	63[a]	1.3	63	1.3	83	3.3	104	6.9	—	—	—	—
					Summer							
Sturgeon Bay	65[c]	1.4	64[c]	1.4	82	3.2	97	5.4	97	5.4	103	6.6
Two Rivers	65	1.4	64	1.4	80	2.9	93	4.8	100	6.2	121	11.6
Port Washington	95	5.1	102	6.5	94	4.9	110	8.3	126	13.3	129	14.2
Waukegan	86	3.7	83	3.2	89	4.1	82	3.2	107	7.8	116	10.2
Saugatuck	80	2.9	50	0.6	60	1.1	80	2.9	82	3.2	93	4.8
Ludington	70	1.8	67	1.6	65	1.5	95	5.1	95	5.1	89	4.2
Frankfort	70[d]	1.8	67[d]	1.6	65[d]	1.5	95[d]	5.1	75	2.4	79	2.8
Green Bay	49	0.5	80	2.9	95	5.1	92	4.7	—	—	—	—

[a]Derived from analyses of the 10–18 m stratum.
[b]Derived from analyses of the 19–37 m stratum.
[c]Derived from analyses of the data off Two Rivers.
[d]Derived from analyses of the data off Ludington.

depth (Table 6) and water column stratification. Based on stratification by bottom depth, approximately 13.7% of total fish biomass was in Green Bay. Confidence intervals by region ranged from approximately 8 to 51% of the mean using bottom depth stratification and from 9 to 26% of the mean using water column stratification. The biomass within various regions ranged from 3.0 to 13.2 $g \cdot m^{-2}$ (Table 4). Highest biomass densities were in Green Bay and in the lake proper off Sturgeon Bay and Frankfort in the north and off Waukegan. Biomass increased by about 1.4-fold between spring and summer (vertical stratification). Green Bay contributed 35.3% of "new" biomass. Lakewide, the pelagic biomass was estimated during day at 13.0 ± 4.5 kt and involved principally small fishes averaging 1.2 g in weight and 62 mm in length (R. L. Argyle, unpubl. data). Evidently, few of the smaller fishes migrated to the bottom during daytime.

Fish Abundances Extrapolated to Other Areas

We believe that although warmwater fishes may be occasionally concentrated in water less than 3 m deep, our lack of sampling at these depths did not lead to large underestimates of total fish numbers and biomass. Water shallower than 3 m makes up less than 1.5% of total lake area and less than 0.03% of the lake volume. If we assume that fish densities between 0 and 3 m were five times denser than the measured fish densities in the adjacent 3–9 m strata, the overall numerical estimate would increase by only 10.8% in spring and 6.7% in summer; biomass would increase 10.4 and 4.8% (Table 6).

We used the data from our incomplete sampling in water deeper than 110 m to compute what we believe to be reasonable estimates of fish numbers and biomass in those depths. Hatch et al. (1981) estimated that 10% of the biomass would be in water greater than 110 m during fall, when fish are generally located further offshore than during our summer sampling period (Wells 1968). To approximate fish abundance in water beyond the 110-m contour, we used the average density of fishes along transects which extended beyond the 110-m contour. In spring, we sampled in water deeper than 160 m off Frankfort, Sturgeon Bay, Ludington, and Two Rivers. Average fish density in these regions beyond 110 m was 0.0986 $fish \cdot m^{-2}$. We assumed that this density was representative of all water deeper than 110 m and that the mean fish weight (11.9 g) was the same as that for the adjacent 74–110 m stratum. If these assumptions were valid, the total increase in numbers and biomass of fishes was 4.9 and 11.1%, based on the vertical stratification (Table 6). For the summer estimate, we used the average fish densities off Two Rivers and Port Washington at depths over 110 m (0.275 $fish \cdot m^{-2}$, mean weight 7.8 g) to estimate fish densities in water deeper than 110 m, except for regions off Sturgeon Bay and Frankfort. A dense scattering layer of fishes was located in epilimnial water and within the top part of the thermocline in waters deeper than 130 m off Frankfort (Fig. 3) and Sturgeon Bay. The fishes in this layer were a mixture of young bloater and alewife with an estimated length of 81 mm and weight of 2.9 g. Fish densities in this layer were as high as 6.89 $fish \cdot m^{-2}$ but averaged 4.70 $fish \cdot m^{-2}$ in

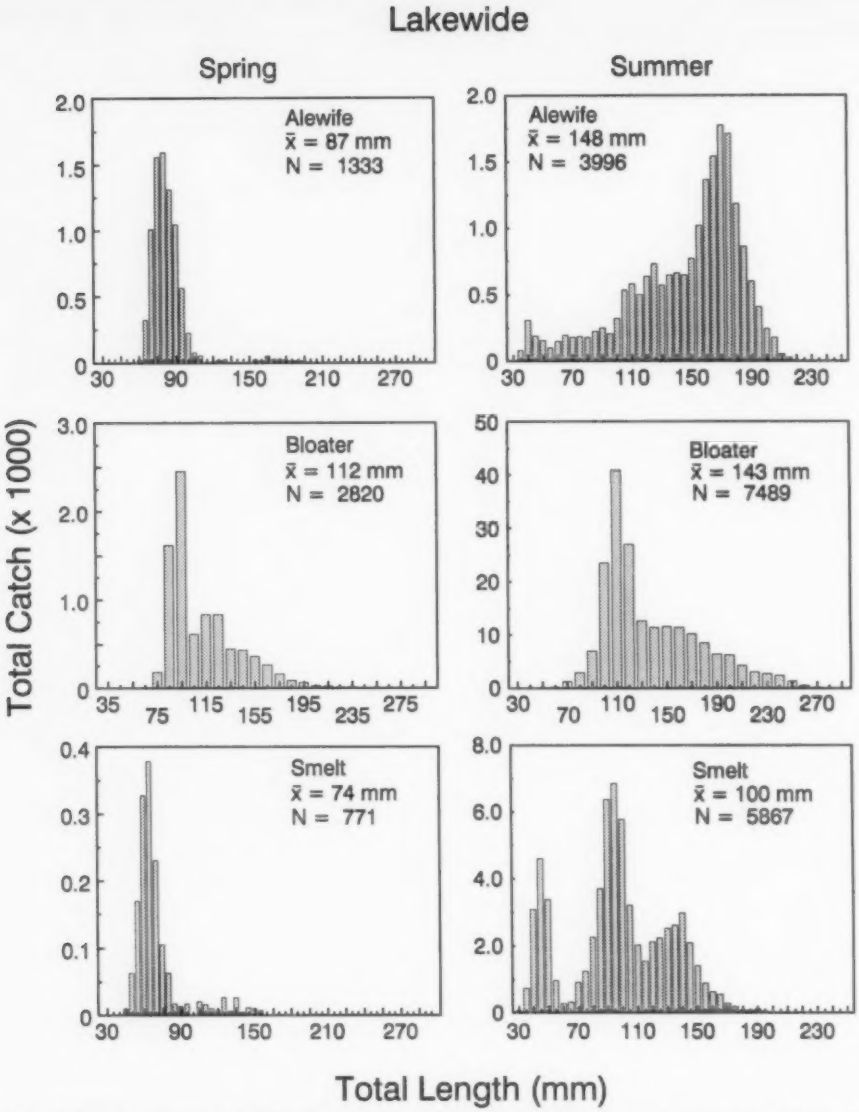

FIG. 5. Length–frequency distribution of alewife, bloater, and rainbow smelt summarized from all bottom trawls taken during the day for spring and summer 1987. *N* represents the number of fishes measured. The vertical axes are the actual trawl catches.

all waters over 110 m deep in these regions. Total number of fishes in water deeper than 110 m off Sturgeon Bay and Frankfort combined was 15.2×10^9 and in all other regions combined was 4.9×10^9. The corresponding biomass estimates were 44.6 and 38.0 kt, respectively. Based on vertical stratification, the inclusion of the deep water increased the number of fishes by 17.3% and the biomass by 26.4% (Table 6).

If we add the values estimated for depths less than 3 m and greater than 110 m, our overall numerical population estimate increased by about 16% in the spring and 24% in the summer (Table 6). Biomass increased by 22% in the spring and 31% in the summer. The lakewide population estimate for summer based on the previous assumptions plus the bottom trawl catches of fishes at night (23.5 kt) yields a total stock estimate of 434.3 kt based on vertical stratification.

Alewife Production and Harvest

We used the total weights of each species of fish taken during the daytime bottom trawling by the R/V *Cisco* to estimate the biomass of each species during summer. Based on the expanded lakewide estimates, biomasses of 60.8 kt of alewife, 34.7 kt of rainbow smelt, and 338.8 kt of bloater were derived. Using the summer estimate of alewife biomass and an updated bioenergetics model for alewife growth (Hewett and Stewart 1989), we calculated the total annual production of alewife in Lake Michigan to be 94.8 kt and estimated the proportion of that production that would be available to predation by stocked trout and salmon (Table 7). Predation rates for trout and salmon (Stewart and Ibarra 1991) were based on 1987 data on salmonine diets. An estimated 60% of available alewife production was removed by salmonine predation (52.9%) and commercial

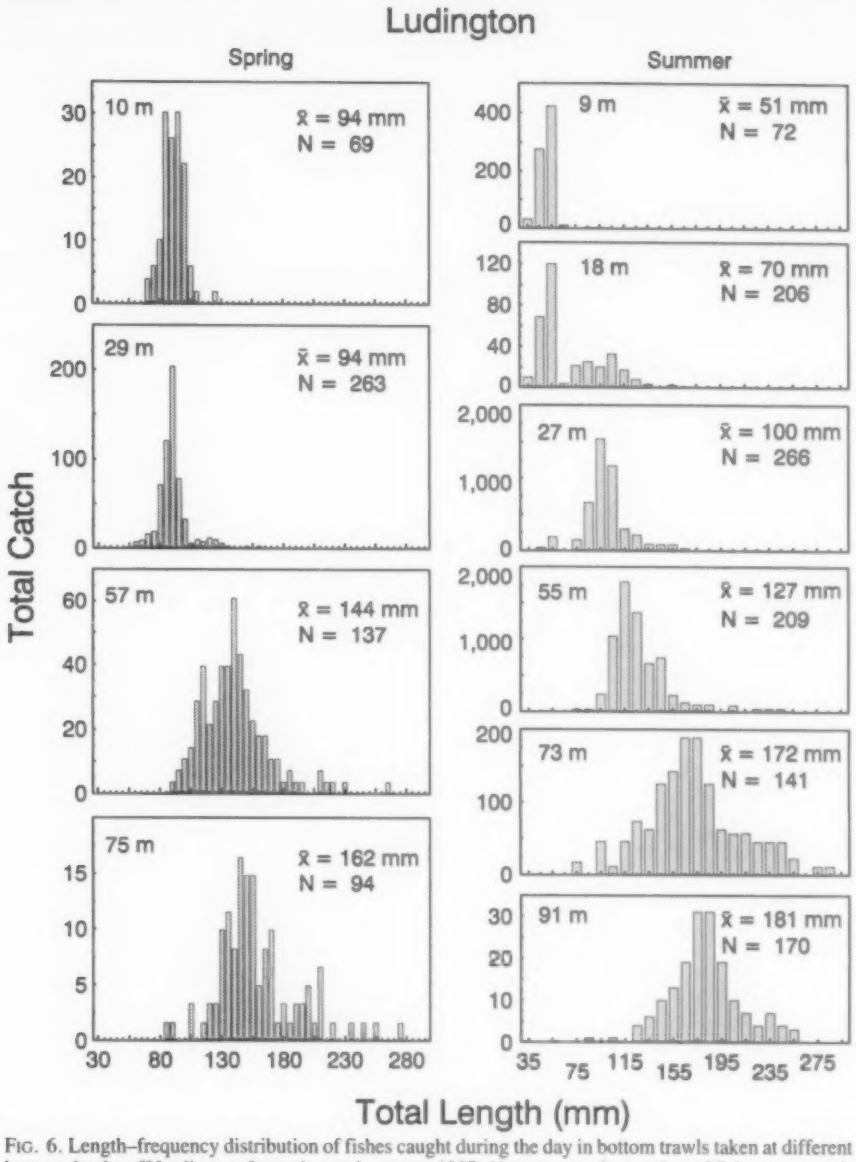

FIG. 6. Length–frequency distribution of fishes caught during the day in bottom trawls taken at different bottom depths off Ludington for spring and summer 1987. *N* represents the number of fishes measured. The vertical axes are the actual trawl catches.

fishing (7.1%). The highest proportion (nearly 75% of total) was taken by the chinook salmon.

Discussion

The numerical and biomass estimates of fishes in Lake Michigan for 1987 are not easily compared with other studies. Few estimates of systemwide abundances of pelagic fishes have been reported, particularly for large freshwater systems. Our estimates of total planktivore biomass were larger than those estimated directly from bottom trawls fished in the fall in Lake Michigan (Brown et al. 1987). The larger estimate seemed reasonable because of the pelagic behavior of younger fishes during the day and trawl avoidance (e.g. Wells 1968). Our lake-wide estimate for total planktivore biomass (excluding Green Bay) of 391.6 kt approximated the biomass estimated for alewife (397.0 kt) in the lake during the mid-1970s (Eck and Brown 1985; Hewett and Stewart 1989) which was based on bottom trawling and estimated survival rates of alewife. Our estimates of mean numbers of fishes per unit surface area in spring and summer 1987 are comparable with overall means of 1.0 fish·m^2 off Two Rivers and Port Washington and 0.5 fish·m^2 in Green Bay during October 1986 (Brandt 1989). Overall, Lake Michigan estimates were larger than the maximum estimated for Lake Ontario (approximately 0.7 fish·m^{-2}) in any one year for 1978–85, but the biomass per unit area was less than that estimated for U.S. waters of Lake Ontario during spring (mean of 10.2 g·m^{-2} for 1978–85) (derived from

TABLE 3. Mean fish densities (fish·m^{-2}) by depth strata, at night, during spring and summer 1987.

Region	Bottom depth (m)					
	0–9	10–18	19–37	38–55	56–73	74–100
			Spring			
Sturgeon Bay	3.01	2.97	7.23	2.11	0.68	0.13
Two Rivers	3.09	0.77	1.91	1.22	1.07	0.42
Port Washington	2.83	4.02	2.26	1.07	1.08	0.20
Waukegan	2.17	4.35	5.84	0.73	0.47	0.39
Benton Harbor	0.97	1.52	1.48	0.62	0.70	0.45
Saugatuck	2.17	1.81	1.89	1.70	0.62	0.33
Ludington	0.82	2.27	0.82	4.72	1.78	0.49
Frankfort	0.33[a]	0.33	0.90	1.84	0.91	0.49
Manistique	0.91	0.75	0.69	1.34	0.34	0.17
Green Bay (upper)	1.31	1.69	1.60	—	—	—
Green Bay (lower)	1.03[a]	1.03	0.56	1.13	—	—
			Summer			
Sturgeon Bay	6.57	5.11	2.86	3.62	4.17	1.00
Two Rivers	1.14	2.48	3.68	0.93	0.41	0.19
Port Washington	3.02	2.54	6.77	1.85	0.83	0.21
Waukegan	0.60	5.95	3.32	3.27	2.29	0.71
Saugatuck	1.13	1.53	8.04	3.09	0.45	1.01
Ludington	1.84	5.65	5.45	3.40	4.47	1.42
Frankfort	1.82	3.72	8.65	3.99	3.63	2.70
Green Bay (upper)	12.56	4.41	2.61	—	—	—
Green Bay (lower)	9.58	3.66	2.90	3.47	—	—

[a]Derived from analyses of the 10–18 m stratum.

TABLE 4. Average fish densities (fish·m^{-2}) and biomass (g·m^{-2}) for each region during spring and summer 1987.

Region	Density		Biomass	
	Spring	Summer	Spring	Summer
Sturgeon Bay	3.76	3.30	12.8	12.9
Two Rivers	1.08	1.11	9.8	3.8
Port Washington	0.87	1.23	6.9	3.0
Waukegan	2.37	2.76	5.8	13.2
Benton Harbor	0.82	—	6.0	—
Saugatuck	0.88	2.42	4.3	5.2
Ludington	1.19	2.50	7.7	9.1
Frankfort	0.86	4.01	4.5	10.0
Manistique	0.72	—	3.8	—
Green Bay (upper)	1.48	7.91	4.9	10.0
Green Bay (lower)	0.82	5.32	1.6	10.7

O'Gorman et al. 1987). The Lake Ontario estimate was based on bottom trawl catches during the day in U.S. waters and did not account for fishes that may have been in the water column during the day. Biomass estimates per unit area in Lake Michigan (lakewide average = 7.21 g·m^{-2} in summer) were somewhat larger than measurements made in the open ocean (e.g. 0.32–3.6 g·m^{-2} in the northern Pacific Ocean, Clarke 1983; Pearcy and Laurs 1966) and in some oligotrophic lakes. For example, Kelso (1988) measured fish biomasses of 0.73 and 2.44 g·m^{-2} in three small (<52 ha) and nutrient-poor lakes of the Turkey Lakes watershed on the Canadian Shield, and Burczynski et al. (1987) estimated biomass densities ranging from 0.25 to 0.85 g·m^{-2} in the rainbow smelt dominated Lake Oahe (152 000 ha). Maximum fish densities in two oligotrophic lakes in northern Wisconsin ranged from 0.2 to 5.1 g·m^{-2} during summer but in the more eutrophic Lake Mendota were as high as 22.3 g·m^{-2} (Rudstam et al. 1987). The Wisconsin lakes were dominated by the cisco (*Coregonus artedii*).

As with all sampling designs and techniques, there are inherent underlying assumptions and potential sources of error in estimating systemwide abundances of fishes. The general limitations of acoustic techniques have been adequately discussed elsewhere (e.g. Thorne 1983). As with all subsampling, we assumed that the sample data were representative of a much larger area. We did not effectively sample near surface (0–3 m), near bottom (1 m), or nearshore (0–3 m) and could only extrapolate fish densities to these areas from measurements taken in adjacent regions. The data stratification procedure also affected total population estimates, particularly when fish distributions were more layered during summer (Brandt 1989). Because fishes are often both vertically and horizontally stratified by size at certain times of the year, a stratification based on both bottom depth and water column depth and perhaps even water temperature (Brandt 1978; Rose and Leggett 1989) may provide a more precise population estimate.

The preceding assumptions and limitations were not believed to have seriously affected our measures of fish abundance in Lake Michigan. Perhaps the most critical assumption concerns the relationship of target strength to fish size. Acoustic techniques directly measure the acoustic target strengths of fishes and then rely on established empirical relationships to estimate actual fish sizes. Target strength is the fraction of incident sound energy that is reflected by a fish back toward the transducer, and factors such as fish behavior and fish orientation will affect the measured target strength. One limitation of in situ methods of measuring fish target strengths (i.e. multi-beam and deconvolution methods) is that fishes must be sufficiently dispersed that their echoes do not overlap (although see Stanton 1985; Stanton and Clay 1986). In some regions of Lake Michigan, fishes were too concentrated to obtain adequate numbers of measurements of fish size.

We assumed that the acoustic reflectivity of all fishes followed Love's (1971) empirical relationship. Love's (1971) equation is the most widely used formula relating the target strength of fish to fish length. This formula was derived by measuring the echo from the dorsal aspect of eight different species of fish. Although this equation often results in reasonably accurate predictions of fish size (Foote 1987), sometimes other equations such as that derived by Love (1977) for the 45° aspect angle provides a better fit, as observed for sockeye salmon (*Oncorhynchus nerka*) (Burczynski and Johnson 1986). Rudstam et al. (1987) derived an equation for cisco (Coregoninae) that was similar to that of Love's (1971) equation. For a target strength of 45 dB, the two equations predict sizes of 97 and 103 mm, respectively. Because most of our targets in Lake Michigan were derived from the coregonine bloater and our estimated sizes were often close to the sizes of fishes taken in trawls, we are reasonably comfortable using Love's (1971) equation. On the other hand, Foote (1987) derived an equation specific to clupeids based on in situ measurements and found clupeid target strengths (at 38 kHz) to be 4.4 dB lower than those derived for various other nonclupeid fishes. This would suggest that our estimate of alewife sizes would be too small. Present day technology is such that we must assume that all fishes in a mixed-species assemblage have, on the average, a particular fish length to acoustic scattering cross-section relationship. If this is not the case, our estimates of mean fish length

TABLE 5. Mean fish densities (number $\times 10^3 \cdot m^{-3}$) measured at different depths in the water column at night during spring and summer 1987.

Region	Water column depth (m)					
	0–9	10–18	19–37	38–55	56–73	74–100
			Spring			
Sturgeon Bay	196.5	184.7	10.3	11.9	2.4	0.6
Two Rivers	66.4	31.3	17.9	6.2	0.8	0.2
Port Washington	123.2	55.8	19.2	6.7	3.8	1.0
Waukegan	99.0	39.6	11.0	3.8	7.0	6.6
Benton Harbor	104.4	23.2	25.7	23.9	1.8	22.6
Saugatuck	37.4	8.1	13.0	10.5	10.9	5.9
Ludington	60.4	12.2	16.8	27.9	13.0	1.4
Frankfort	9.7	6.7	17.6	42.2	21.7	12.2
Manistique	50.0	19.4	15.4	10.1	1.2	0.9
Green Bay (upper)	146.9	8.6	13.2	—	—	—
Green Bay (lower)	40.3	22.7	27.0	51.9	—	—
			Summer			
Sturgeon Bay	619.5	7.2	15.0	2.4	0.6	0.2
Two Rivers	144.2	29.4	6.4	1.1	0.8	0.3
Port Washington	86.5	51.6	27.4	10.5	4.7	0.7
Waukegan	170.7	56.0	64.5	43.1	4.2	3.1
Saugatuck	209.0	115.0	75.4	8.4	3.7	6.3
Ludington	302.3	186.0	80.2	67.1	24.5	11.3
Frankfort	464.8	188.3	85.0	49.1	37.1	5.0
Green Bay (upper)	921.9	72.0	95.9	—	—	—
Green Bay (lower)	1148.6	20.2	38.5	163.4	—	—

TABLE 6. Biomass and numerical abundances (±95% CI) of fishes estimated with acoustics during spring and summer 1987. Density measures were stratified by bottom depth to derive total abundances.

Region	Spring		Summer	
	Number (billions)	Biomass (kt)	Number (billions)	Biomass (kt)
Lake (0–110 m)	38.96	214.0	89.64	270.4
Green Bay	4.45	12.0	26.19	42.8
Subtotal	43.41	226.0	115.84	313.2
±95% CI	±10.07	±55.2	±18.34	±74.3
Lake (>110 m)	2.13	25.1	20.06	82.6
Lake and Green Bay (<3 m)	4.69	23.5	7.76	15.0
Total	50.23	274.6	143.66	410.8

TABLE 7. Comparison of 1987 alewife biomass estimates for Lake Michigan with modelling estimates of available production by that alewife population and removals of alewife by commercial fishing and predation by stocked salmonines.

	Biomass (kt)	Percentage of total biomass
Alewife total biomass	60.8	100.0
Alewife annual total production	94.8	156.0
Alewife production available	83.9	138.0
Alewife removals		
Commercial fishery	4.3	7.1
Predation (model estimates)		
Coho salmon	5.1	8.4
Chinook salmon	27.3	44.9
Lake trout (excluding deep reef)	3.7	6.1
Brown and rainbow trout[a]	9.9	16.3
Total removals	50.3	82.8
(Percentage of available production)		(60.0)

[a]Predation approximation for brown and rainbow trout estimated from average per individual stocked for the other three species.

and fish biomass would be biased. Ideally, if we could attribute each individual target to a particular species either through some acoustic signature (Rose and Leggett 1988) or through allocating the biomass to a particular species by the type of environment from which the target originated, then we could use a different relationship for each species.

One of the more severe limitations of acoustic techniques is the inability to distinguish species directly. Acoustic estimates of abundance of a single species in a mixed-species assemblage will be limited by the level to which relative species composition can be determined. In Lake Michigan, the relative abundances of alewife, rainbow smelt, and bloater are not known but only estimated from bottom trawling. This assumes that there are no differences in availability or catch efficiency among different species or different sizes of individuals within a species. Clearly this is not the case in Lake Michigan because younger individuals are pelagic during the day. Since acoustic measures of the abundance of a species depend directly on weighting density measures by the proportion of the species in the environment, both precision and accuracy of these biomass estimates will be directly proportional to that of the "ground truthing" technique. For example, if trawling suggests that the fish composition (biomass) in an area is 20% species A and 80% species B, but the composition in fact is 10% species A and 90% species B, our abundance estimate of species A would

be 100% too high and our abundance estimate for species B would be 11% too low. The variance about these acoustic estimates corresponds directly to the variance about the estimate of relative species composition.

We could improve abundance measures of different species by defining species-specific distribution patterns and then allocate biomass estimates to different species on the basis of the type of habitat from which echoes were received. Consistent patterns in habitat-derived patchiness (e.g. fishes occupying different temperatures) could help identify fish targets if different species or life history stages occupy different habitats. Such habitat-derived patchiness has not been fully used in the design, execution, or statistical treatment of acoustic surveys for stock assessment. New procedures are also evolving (Rose and Leggett 1988; Brandt 1989) to use acoustic signatures directly to identify spatially segregated fishes.

The population estimates derived for spring and summer were biologically realistic. We expected that the fish biomass during the summer would be higher than in the spring due to fish growth and recruitment and that the increase in numbers should be greater than the increase in biomass. Overall, the planktivore biomass was also within the range that might be predicted from system-level models based on phytoplankton and zooplankton production (Sprules et al. 1991).

The acoustic data also provided certain insights to the distributional ecology of pelagic planktivores in Lake Michigan. Younger, smaller fishes were shallower in the water column and closer to shore than larger individuals. Furthermore, smaller fishes did not appear to migrate to the bottom during the day. These results are consistent with other observations of alewife (Wells 1968; Argyle 1982; Brandt 1980), rainbow smelt (Brandt et al. 1980; Crowder et al. 1981), and bloater (Crowder and Crawford 1984) in the Great Lakes that earlier life stages are generally found in warmer water than adults and are largely pelagic during both day and night. Acoustic surveys taken during the day may provide a method for estimating the abundances of these hard-to-sample younger fishes.

The highly eutrophic parts of Green Bay contained the highest numerical density of fishes during summer. These fishes were mainly small and probably young-of-the-year. It is not known whether fishes migrate into Green Bay from the lake proper to spawn or whether recruitment is more successful in the more productive Green Bay. Densities of fishes in Green Bay in fall 1986 and spring 1987 were similar to those within the lake, which raises questions concerning the fate of the high densities of fishes in Green Bay in summer. Do these young fishes migrate into the lake, to nearshore or unsampled areas, or are they subject to higher mortality than pelagic fishes in the lake. Further research is needed to evaluate the contribution of such embayments to overall production within Great Lakes ecosystems.

The distribution of pelagic fishes in 1987 was quite different from that of the mid-1970s when the lake was dominated by alewife. The highest densities of pelagic fishes in the mid-1970s were located near the thermocline or in the epilimnion during summer at night (Brandt 1978; Janssen and Brandt 1980; Brandt et al. 1980). Large biomasses of fishes, mostly bloaters, now reside in hypolimnial waters near 8°C (Brandt 1989). This shift in the distribution of planktivore biomass has implications for planktivore availability to salmonine predation (Stewart and Ibarra 1991) as well as for consumer control of lower trophic levels (e.g. McDonald et al. 1990).

The apparent concentration of alewife near Two Rivers, specifically, and the western shore of Lake Michigan, in general, during the spring suggests that alewife undertake seasonal, lakewide migrations. Although this inference is based on observations during 1 yr only, the conclusions are not surprising. Atlantic coast, oceanic alewife migrate great distances (Neves 1981) and also move westerly during spring. Whether alewife migrations are a remnant of oceanic behavior or whether these fishes are responding directly to local environmental factors is not known. The Two Rivers area is physically unique in that it is near the intersection of the general northern basin and southern basin gyres and it is also located in a region frequented by upwelling, which may provide enhanced prey abundances. Two Rivers was the coldest area during both sampling periods.

Estimates of alewife production and salmonine predation suggest that the alewife population is being exploited at a very high rate and the lack of available prey apparently is reflected in reduced salmonine growth (Stewart and Ibarra 1991). Our estimates of the proportion of alewife being consumed by predation or commercial fishing are considered minimum estimates. The alewife population estimate used was maximized, particularly by including the 0–3 m expanded density assumptions. We also assumed that all postlarval alewife were available for salmonine consumption. Clearly, the young-of-the-year bloater and the yearling alewife that were concentrated in warmer offshore waters in summer would be less available for salmonine predation, particularly for species such as the lake trout. Our estimates were also based on lakewide averages and did not consider the finer-scale spatial disparities that may exist in prey production and predation rate. Alewife production in warm water may not be available to cooler-water predators; and alewife production that occurs, for example off Manistique, may not be exploitable by salmonines concentrated in the southern basin of the lake.

Much of the lakewide planktivore biomass (i.e. bloater) is unavailable to salmonines for food without the cost of feeding at temperatures which are not optimal for growth. Finer-scale compartmentalization of production and predation may be required to evaluate food web processes in large-scale systems such as the Great Lakes. Until such time as the trout and salmon switch to alternative prey, it is clear that the alewife population is not sufficient to support present stocking rates and high growth rates of salmonines.

The spatial and temporal patchiness of pelagic planktivores in the Great Lakes indicates that population assessment techniques should employ continuous sampling methods. Underwater acoustics is particularly suitable to the Great Lakes because planktivore communities are characterized by only two to three dominant species. System-level quantification is critically needed in the Great Lakes (Lewis et al. 1987; Leach et al. 1987) to understand the processes affecting lakewide production. The ability to measure the complete abundance of pelagic planktivores throughout Lake Michigan should provide us with a tool that is useful not only for estimating the level of piscivory that can be supported in the lake but also for quantitatively examining the effect these planktivores can have on lower trophic levels (Scavia et al. 1988; Hewett and Stewart 1989) and on the system as a whole.

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Predation and Production by Salmonine Fishes in Lake Michigan, 1978–88[1]

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A marked decline of alewife (*Alosa pseudoharengus*) in Lake Michigan during 1981–83 led to diet shifts by coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) from feeding primarily on large alewife to eating proportionately more immature alewives and other prey. Diets of lake trout (*Salvelinus namaycush*) did not change greatly during that period. Population biomass conversion efficiency averaged 24.5% for coho and 16.6% for lake trout. Chinook salmon suffered an apparent 20% decline in gross conversion efficiency of biomass (25.1 to 20.8%) and a 25% decline in average weight of sport-caught fish. We infer that chinook salmon growth was inhibited by insufficient forage available to them. A simulation of chinook salmon feeding on bloater (*Coregonus hoyi*) at 8°C suggested that such behavior could lead to further declines in growth rates. Extension of modeling results to include approximations for brown trout (*Salmo trutta*) and rainbow trout (*O. mykiss*) revealed peaks in total annual salmonine predation of 71 000 t in 1983 and 76 000 t in 1987. The alewife was 70% of all prey eaten by salmonines in 1987–88. Lakewide gross production by salmonines was 15 300 t (or 0.27 $g \cdot m^{-2}$) in 1987. Ratios of annual gross production to average monthly population biomass were 1.6 for chinook, 1.15 for coho, and only 0.6 for lake trout.

Une chute importante de la population de gaspareau (*Alosa pseudoharengus*) dans le lac Michigan de 1981 à 1983 a fait en sorte que les saumons coho (*Oncorhynchus kisutch*) et quinnat (*O. tshawytscha*) y ont modifié leur régime alimentaire : se nourrissant principalement de gaspareau de grande taille, ils sont passés à une plus forte proportion de gaspareaux immatures et d'autres proies. Le régime des touladis (*Salvelinus namaycush*) n'a pas beaucoup changé durant cette période. Les rendements moyens de la bioconversion chez les populations de coho et de touladi étaient de 24,5 et 16,6 %, respectivement. Le rendement brut de bioconversion du quinnat a connu une chute apparente de 20 % (de 25,1 à 20,8 %), et le poids des quinnats pêchés par les pêcheurs sportifs étaient en moyenne de 25 % inférieur. Nous en concluons que la croissance des quinnats a été inhibée en raison de ressources alimentaires insuffisantes. Un modèle simulant la croissance du saumon quinnat soumis à un régime de saumon de fumage (*Coregonus hoyi*) à une température de 8°C a montré que dans de telles conditions, la croissance du quinnat pourrait être davantage ralentie. Avec des approximations dérivées des résultats de ce modèle pour la truite brune (*Salmo trutta*) et la truite arc-en-ciel (*O. mykiss*), on obtient des valeurs maximales de prédation annuelle totale par les salmonidés de 71 000 t en 1983 et de 76 000 t en 1987. Le gaspareau représentait 70 % de toutes les proies consommées par les salmonidés pour la période 1987–1988. Pour l'ensemble du lac, la production brute des salmonidés était de 15 300 t (ou 0,27 $g \cdot m^{-2}$) en 1987. Les rapports entre la production brute annuelle et la biomasse moyenne mensuelle des populations étaient de 1,6 pour le quinnat, 1,15 pour le coho et seulement 0,6 pour le touladi.

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The highly valued, artificially maintained Pacific salmon populations of Lake Michigan appear to be undergoing striking changes. Large chinook salmon (*Oncorhynchus tshawytscha*) experienced spring die-offs in southern Lake Michigan during 1988 and 1989 (D. Brazo, Indiana Department of Natural Resources, Michigan City, IN, pers. comm.). Sport angler harvests and returns of adult Pacific salmon to weirs in Michigan also declined recently, suggesting an increase in mortality rates (R. Hay, Michigan Department of Natural Resources, Cadillac, MI, pers. comm.). Average weight of chinook salmon in the Wisconsin sport catch has declined since the early 1980's (see below). These changes have led to reduced economic returns to sport fishery support services, discontent among sport anglers (Huggler 1989), and pressure to compensate by increasing salmonine stocking rates and reducing commercial harvest of prey fish stocks (Keller et al. 1989).

The prey fish assemblage in Lake Michigan has changed dramatically over the past decade, shifting from one strongly dominated by alewife (*Alosa pseudoharengus*) to one dominated by bloater (*Coregonus hoyi*) (Jude and Tesar 1985; Wells 1985; Kitchell and Crowder 1986; Eck and Wells 1987). In spite of those changes, alewife remain the primary prey of the Pacific salmon (Stewart et al. 1981; Hager 1984; Eck and Brown 1985; Jude et al. 1987). A sharp decline in alewife in 1981–83 and their subsequent failure to recover to biomass levels of the mid–

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1970's may explain, in part, present difficulties of the salmon. Uncertainties remain, however, because of incomplete quantification of system-wide prey production compared with salmonine predation. What is the carrying capacity of Lake Michigan for salmonine fishes? How has that changed in relation to recent prey fish population dynamics? Most likely the interactions are complex and nonlinear. Recent synthesis papers emphasize the importance of managing Great Lakes fishes with an ecosystem perspective (Spangler et al. 1987; Steedman and Regier 1987) and limitations of the information available to accomplish that task (Lewis et al. 1987; Leach et al. 1987). This paper provides a whole-system perspective on salmonine predation and production as a contribution towards the information base needed to understand the dynamics of Great Lakes ecosystems.

Objectives of this study are to estimate (1) total salmonine predation pressure on Lake Michigan prey populations for 1978–88 through a modeling synthesis of available data, (2) the effects of recent diet changes upon population conversion efficiencies for coho salmon (*Oncorhynchus kisutch*), chinook salmon, and lake trout (*Salvelinus namaycush*), and (3) total salmonine production and production to mean biomass ratios in Lake Michigan. Our intent is to update and extend the analyses of Stewart et al. (1981), Eck and Brown (1985), and Kitchell and Crowder (1986) through 1988 to provide a solid foundation of best-available predation and production estimates. These contribute to a comparison of salmonine predation and alewife production (Brandt et al. 1991), thereby providing a basis for making informed management decisions (e.g. Krueger and Dehring 1986; Ney 1990). Our results can also facilitate system-level modeling of food web dynamics (e.g. Scavia et al. 1988) and evaluation of biomass size spectrum theory (Sprules et al. 1991).

Methods

We modeled the bioenergetics of lake trout using the energy balance equations and parameters of Stewart et al. (1983). Models for coho salmon and chinook salmon differed from that for lake trout but resembled a model for sockeye salmon (*Oncorhynchus nerka*) (Beauchamp et al. 1989) in that we modeled temperature dependence of maximum consumption using the function of Thornton and Lessem (1978). Models for all three species were implemented using the microcomputer program of Hewett and Johnson (1987). A similar model for sockeye salmon was corroborated by independent estimates of feeding rates in three different systems (Beauchamp et al. 1989). Physiological parameters used for coho and chinook salmon (Table 1) are the same as those used by Stewart et al. (1981) and Kitchell and Hewett (1987). Parameters for temperature dependence of maximum consumption were estimated by hand-fitting the functions of Thornton and Lessem (1978) to laboratory observations on coho salmon (Fig. 1). In the following sections, we provide additional documentation of data sources and assumptions for thermal distribution, energy density, swimming speed, population numbers, survival and growth rates, and diet composition.

Thermal Distributions

Juvenile coho and chinook salmon both preferred temperatures of 12–14°C when exposed to a vertical gradient in the laboratory (Brett 1952). Jude et al. (1987) found that juvenile

TABLE 1. Symbols and estimated physiological parameter values used to implement energetics models for coho and chinook salmon. Parameters are for equations in Stewart et al. (1983) and Thornton and Lessem 1978; θ_{1-4} and K_{1-4}).

Symbol	Parameter description	Parameter value	References
	Consumption, C_{max}		
a	Intercept: C_{max} at $(\theta_2+\theta_3)/2$	0.303 ($g \cdot g^{-1} \cdot d^{-1}$)	Beauchamp et al. 1989; from Brett 1971
b	Coefficient: C_{max} vs. weight	−0.275	Beauchamp et al. 1989; from Davis and Warren 1968; Edsall et al. 1974
θ_1	Temperature for K_1	5	Stewart 1980; from Edsall et al. 1974
θ_2	Temperature for K_2	15	Stewart 1980; from Edsall et al. 1974
θ_3	Temperature for K_3	18	Stewart 1980; from Edsall et al. 1974
θ_4	Temperature for K_4	24	Stewart 1980; from Edsall et al. 1974
K_1	Proportion C_{max} at θ_1	0.36	Stewart 1980; from Edsall et al. 1974
K_2, K_3	Proportion C_{max} at θ_2, θ_3	0.98	Stewart 1980; from Edsall et al. 1974
K_4	Proportion C_{max} at θ_4	0.01	Stewart 1980; from Edsall et al. 1974
	Metabolism, R		
α	Intercept: R	0.00264 ($g\ O_2 \cdot d^{-1}$)	Stewart 1980; from Rao 1968, 1971
β	Coefficient: R vs. weight	−0.217	Stewart 1980; from Rao 1968, 1971
ρ	Coefficient: R vs. temperature	0.06818	Stewart 1980; from Rao 1968, 1971
ν	Coefficient: R vs. swimming speed	0.0234	Stewart 1980; from Rao 1968, 1971
	Swimming speed, U		
ω	Intercept: U	9.7 ($cm \cdot s^{-1}$)	Stewart 1980; from Wiehs 1973
δ	Coefficient: U vs. weight	0.13	Beauchamp et al. 1989
ϕ	Coefficient: U vs. temperature	0.0405	Beauchamp et al. 1989; from Griffiths and Alderdice 1972; Glova and McInerney 1977

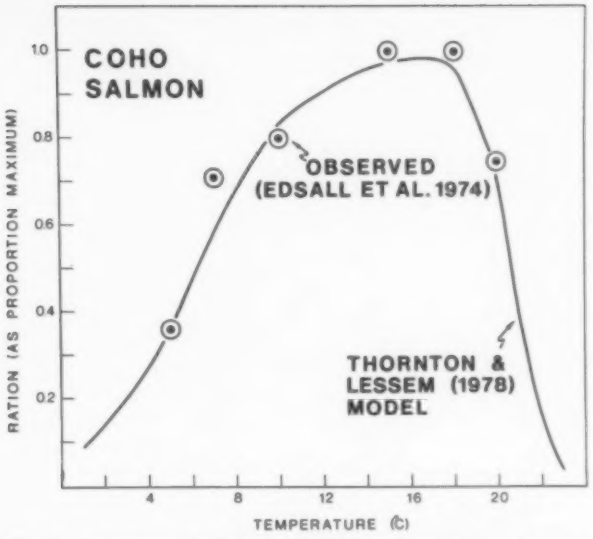

FIG. 1. Temperature dependence of maximum consumption for coho salmon, comparing predicted values from Thornton and Lessem's (1978) model with observed values from Edsall et al. (1974).

salmonines other than lake trout occupy the nearshore zone of Lake Michigan where they feed on surface insects at temperatures often exceeding 20°C. Based on radiotagged adult fishes tracked in Lake Ontario during spring and summer, coho salmon occupied temperatures of 9.3 ± 2.1°C (n = 16) and chinook salmon occupied 11.1 ± 1.9°C (n = 7) (Haynes and Keleher 1986). Those differences were not significant. Haynes and Keleher (1986) did note, however, that coho salmon tended to occupy nearshore and surface waters more than chinook. During the period of midsummer stratification in Lake Ontario, chinook salmon were found in or just above the thermocline (average 14.4°C, Olson et al. 1988). We modeled both species using midlake epilimnion water temperatures from Lake Michigan (Ayers 1962) and the assumption that the salmon would occupy the warmest waters available up to but not exceeding their preferred temperature (see Stewart et al. 1983, fig. 4, for example). Based on the foregoing information, we assumed a preference of 12°C for coho, 11°C for age 1+ and older chinook, and 18°C for age 0+ chinook.

Energy Density

Seasonally varying energy density of alewife in the salmonine diets was modeled based on Stewart and Binkowski (1986, fig. 3), and that for other prey types follows Stewart et al. (1983). The following relationships based on simple linear regressions were used to approximate weight dependence of energy density in Lake Michigan coho salmon (Stewart 1980). From data for coho salmon (Reinert and Bergman 1974), we estimated

$$(1)\quad L = 5.08 + 0.00207\,W$$

where L is percentage fat content of the entire fresh fish and W is wet weight (grams). From data on sockeye salmon (Brett et al. 1969), we estimated

$$(2)\quad Q = 3346 + 476\,L$$

where Q is energy density (joules per gram). Combining equations 1 and 2, we get

$$(3)\quad Q = 5763 + 0.986\,W.$$

Equation 3 also was applied to chinook salmon up to 4 kg. We assumed that chinook salmon larger than 4 kg would increase their fat and energy content per unit weight at a slower rate, resembling the pattern observed for lake trout (Stewart et al. 1983). Large chinook salmon can have 7–16% fat in their muscles (Green 1913; Stansby 1976), which would typically be less than in the fish as a whole. At 4 kg, whole-fish fat content of a Lake Michigan coho salmon approaches 14% (Reinert and Bergman 1974). To allow for additional, modest increases of fat in very large chinook salmon, we assumed a value of 20% fat for a 10-kg chinook. Under that assumption, energy density at 10 kg might approach 12 866 $J \cdot g^{-1}$, and the linear increase between 4 and 10 kg would be

$$(4)\quad Q = 7598 + 0.527\,W.$$

Swimming Speed

Boisclair and Leggett (1989) suggested that consumption estimates based on bioenergetics models of actively foraging fishes may be in error if in situ measures of activity have not been made. They conceded, however, that an approach like that used here may be best for piscivorous fishes that consume large prey which require long digestion times. The submodel for swimming speed (Stewart et al. 1983; Beauchamp et al. 1989) and associated parameters (Table 1) were based on a synthesis of theoretical and empirical estimates of weight and temperature dependence of swimming speed for various salmonines (Stewart 1980). Pacific salmon in particular are amenable to such a model because they have evolved to swim long distances in effectively bottomless habitat searching for active, pelagic prey.

Field observations on radio-tagged salmonines in Lake Ontario indicated swimming speeds (centimetres per second) of 17 for 1.4- to 5.0-kg coho salmon, 13 for 1.8- to 9.0-kg chinook salmon, and 14 for 1.4- to 5.5-kg rainbow trout (*Oncorhynchus mykiss*) (Haynes and Keleher 1986; Haynes et al. 1986). These field estimates, based on relocations of fishes made at 24- to 72-h intervals, should represent minimum values. Predictions of our model for fishes at comparable weights and temperatures (9.3–11.1°C) range from 36 to 49 $cm \cdot s^{-1}$ and correspond to active metabolic rates of 2.3–3.1 times standard metabolism.

Salmonine Populations

Salmonine stocking data (Table 2) were compiled from reports and personal communications from M. Hansen (Wisconsin Department of Natural Resources, Madison, WI), B. McClay (Michigan Department of Natural Resources, Lansing, MI), R. Hess (Illinois Department of Conservation, Chicago, IL), D. Brazo (Indiana Department of Natural Resources, Michigan City, IN), and R. Eshenroder (Great Lakes Fishery Commission, Ann Arbor, MI). We corrected the numbers of lake trout stocked for overwinter mortalities of fall fingerlings and for those stocked at depths where alewife are uncommon (Table 2). The survival rate assumed for all age classes of lake trout was 52% (Eck and Brown 1985), in contrast with Stewart et al. (1981, 1983) who assumed survival of 63% for the first four years, and 45.3% for the older age classes (following Rybicki and Keller 1978). Survival rates for Pacific salmon (Fig. 2) follow Stewart et al. (1981).

TABLE 2. Numbers stocked and estimated populations of salmonine fishes in Lake Michigan. Simulations for lake trout, coho salmon, and chinook salmon were based on populations estimated from numbers stocked and mortality assumptions given in the text. Lake trout yearlings include 41.7% of previous year's fall fingerlings (e.g. Yrlg. equiv., below), a correction to account for overwinter mortality of the fall fingerlings (Elrod et al. 1988). We excluded "Deep reef" lake trout that were stocked on the Milwaukee Reef complex where diets and growth rates are noticeably different from those of shallow-dwelling fishes (M. Miller, Wisconsin Department of Natural Resources, Madison, WI, pers. comm.). Rainbow and brown trout yearling numbers also include yearling equivalents approximated as 41.7% of previous year's fall fingerlings.

	Numbers stocked (thousands)									Population		
	Lake trout					Rainbow trout		Brown trout				
Year	Yearlings	Yrlg. equiv.	Deep reef	Coho salmon	Chinook salmon	Yearlings	Yrlg. equiv.	Yearlings	Yrlg. equiv.	Coho salmon	Chinook salmon	Lake trout
65	1274	0	0	0	0	25	0	0	0	0	0	1274
66	1717	0	0	660	0	155	0	22	0	660	0	2379
67	2179	0	0	1732	802	53	13	58	7	1942	802	3701
68	1995	119	0	1201	887	365	18	84	5	1753	1 271	3919
69	1999	0	0	3199	718	397	0	166	72	3582	1 305	4051
70	1960	0	0	3542	1904	500	9	136	20	4561	2 481	4094
71	2345	0	0	2751	2247	914	17	803	39	3880	3 363	4519
72	2722	0	0	2623	1819	832	17	222	19	3500	3 329	5206
73	2469	85	0	2204	3046	1882	141	1840	301	3040	4 500	5228
74	2355	83	0	3231	3578	2012	127	792	142	3933	5 555	5243
75	2505	52	0	2445	4280	1644	57	752	122	3475	6 732	5378
76	2384	42	277	2664	3302	1521	86	675	22	3443	6 280	5231
77	2322	0	0	3014	2819	1227	164	963	169	3863	5 508	5094
78	2493	18	0	2631	5365	750	58	806	151	3591	7 670	5193
79	2454	27	0	3999	5085	1566	519	973	361	4837	8 444	5210
80	2474	50	199	2868	6106	1811	610	944	250	4142	9 817	5234
81	2049	112	93	2452	4798	1766	608	970	256	3366	9 111	4817
82	2305	220	14	2180	6035	1480	326	851	190	2961	9 911	4859
83	1956	249	555	2360	6180	1516	589	1557	625	3055	10 450	4531
84	886	13	282	2745	7170	2066	620	1373	622	3497	11 673	3291
85	1945	96	865	2659	5955	2011	672	1233	437	3534	11 044	3702
86	2321	531	684	2177	5607	2059	177	1186	422	3024	10 326	4292
87	1602	343	714	2291	5485	1941	396	909	278	2985	9 856	3875
88	1359	10	544	2572	5739	1285	121	1125	302	3302	9 900	3422

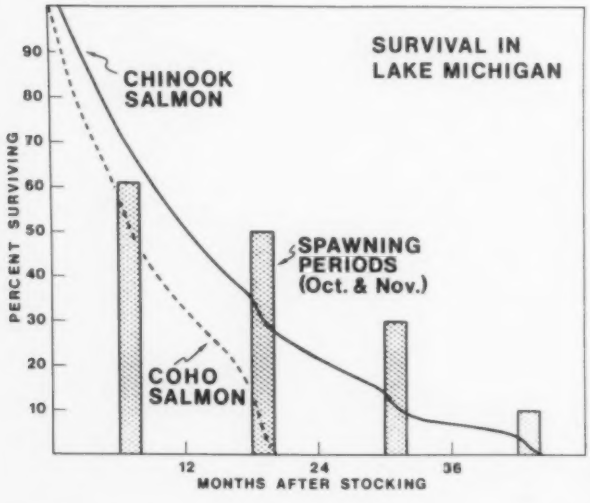

FIG. 2. Comparison of estimated survivorship curves for coho and chinook salmon in Lake Michigan. Proportion surviving various intervals are from Stewart et al. (1981, table 3).

We extended our modeling estimates of predation and production to get approximations for the whole-lake salmonine assemblage by assuming that contributions by an individual rainbow trout or brown trout (*Salmo trutta*) were approximately equal to the average of those for the three modeled salmonines (Stewart et al. 1981). We used stocked numbers of yearling rainbow and brown trout, including 41.7% of previous year's fall fingerlings (Table 2). Using the lake trout correction factor for fall fingerlings is arbitrary, but perhaps is an improvement over use of the raw numbers stocked. We made no attempt to evaluate predation by naturally spawned salmonines because data were too incomplete.

Growth Rates

Weights-at-age on 1 July for typical lake trout simulated by Stewart et al. (1983, based on Rybicki and Keller 1978) averaged somewhat greater than weights reported by Eck and Brown (1985) for fish on 15 May. We forced the growth simulation to fit Eck and Brown's (1985) weights for 15 May by reducing ration (as a proportion of maximum ration) and then used the lowered rations in the model to predict weights on 1 July for each age class. That procedure revealed that weights reported by Eck and Brown (1985) averaged 79% of those used by Stewart et al. (1983). For our analyses, we lowered weights 21% to approximate the slower growth rates observed by Eck and

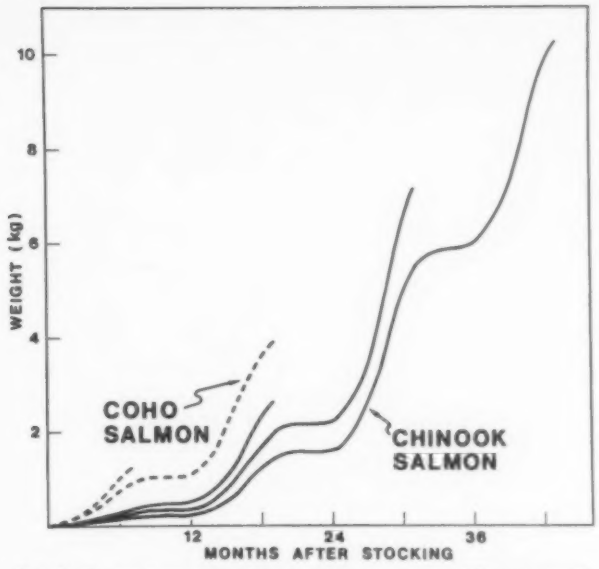

FIG. 3. Comparison of predicted weight-at-age for different growth forms of coho and chinook salmon in Lake Michigan during 1978–81. Weights at the end of various intervals are from Stewart et al. (1981, table 3).

Brown (1985). Analyses of mean weight of lake trout in the Wisconsin sport catch by Hansen (1986) and of our own weight data suggest an increase in recent years. For example, average weight was about 3.17 kg in 1983 (n = 296), 3.87 in 1985 (n = 177), and 3.60 in 1987 (n = 79). That apparent trend is likely due to more older fish in the population or retention by anglers of fewer small fish. Keller et al. (1989) noted that lake trout growth has declined in southern Lake Michigan but remained reasonably stable in central and northern parts of the lake. If that pattern applies lakewide, then our predation estimates for lake trout would be less than actual values.

For simulations of coho and chinook salmon in 1978–82 (Fig. 3), we used weights-at-age from Stewart et al. (1981). To evaluate trends in body weight following the 1981–83 alewife decline, we calculated mean weight of sport-caught fishes in western Lake Michigan for each year from 1982 through 1988. That analysis revealed that weights of coho salmon in 1983, 1985, and 1987 were not different from 1982, but weights in 1984, 1986, and 1988 averaged about 82% of those in during the other four years (n = 1774 over the 7-yr period). We thus lowered coho weights-at-age from Stewart et al. (1981) by 18% for the three slow-growth years. We did a similar analysis for chinook salmon (n = 1098 over the 7-yr period) but used only June and July data to remove apparent biases due to seasonal differences in size structure of the catch in different years. That analysis revealed that 1983 was similar to 1982 (average weight for those two years, 5.9 kg), weights in 1987 were 86% of 1982, and weights in 1984–86 and 1988 were all about 71% of 1982. We lowered weights-at-age for chinook salmon in the 1984–88 simulations by the appropriate percentage reductions of nominal values in Stewart et al. (1981).

Diets

1978–81

Information on proportional diet composition for Lake Michigan salmonines (Tables 3–6) can be divided into the periods 1978–81 and 1982–88. Diet data for 1978–81 are from Stewart et al. (1981, 1983) with modifications to reflect more recently published data. For age 0+ chinook and age 1+ coho salmon, diets (Table 3) were adjusted to include higher proportions of invertebrates (P_{INV}) and fish other than alewife (P_{OTH}), with corresponding reductions in proportions of small (P_{SMA}, <8.0 g) and large (P_{LGA}, ≥8.0 g) alewife, reflecting the results of Jude et al. (1987). For lake trout, diets for age 1+ (Table 3) were unchanged from Stewart et al. (1983), but those for ages 2+ to 9+ were adjusted to include data on winter diets from Eck and Wells (1986). Thus, we used a single diet table for each salmonine species for the years 1978–81; between-year differences in predation rates for those years only reflect changes in population structure.

TABLE 3. Proportional diet composition (P, by wet weight; subscripts are INV for invertebrates, OTH for fish other than alewife, SMA for alewife under 8 g, and LGA for alewife greater than or equal to 8 g) for juvenile salmonines in Lake Michigan during various times of the year. Estimates are based on Stewart et al. (1981, 1983), with chinook and coho diets adjusted to reflect results of Jude et al. (1987) and lake trout diets for age 2+ adjusted for winter data of Eck and Wells (1986; i.e. simulation days 168 and 274). Simulation day 1 is 1 May for chinook salmon, 1 April for coho salmon, and 1 July for lake trout.

Simulation days		Food type				
Start	End	P_{INV}	P_{OTH}	P_{SMA}	P_{LGA}	Year(s)
Chinook age 0+						
1	61	0.97	0.03	0.00	0.00	1978–88
62	123	0.50	0.40	0.10	0.00	1978–88
124	365[a]	0.00	0.40	0.60	0.00	1978–81
124	365[a]	0.00	0.30	0.32	0.38	1982
124	365[a]	0.00	0.37	0.63	0.00	1983
124	365[a]	0.00	0.30	0.32	0.38	1984
124	365[a]	0.00	0.37	0.63	0.00	1985
124	365[a]	0.00	0.07	0.75	0.18	1986
124	365[a]	0.00	0.37	0.63	0.00	1987
124	365[a]	0.00	0.07	0.75	0.18	1988
Coho salmon, age 1+						
1	153	0.60	0.29	0.11	0.00	1978–88
154	365	0.00	0.60	0.26	0.14	1978–88
Lake trout, age 1+						
1	123	0.75	0.21	0.04	0.00	1978–88
124	153	0.30	0.66	0.04	0.00	1978–88
154	335	0.30	0.54	0.16	0.00	1978–88
336	365	0.30	0.13	0.57	0.00	1978–88
Lake trout, age 2+						
1	123	0.10	0.53	0.00	0.37	1978–88
124	153	0.10	0.31	0.59	0.00	1978–88
154	168[a]	0.00	0.10	0.90	0.00	1978–88
169	274[a]	0.00	1.00	0.00	0.00	1978–88
275	365[a]	0.10	0.53	0.00	0.37	1978–81
275	365[a]	0.00	0.31	0.07	0.62	1982
275	365[a]	0.00	0.31	0.19	0.50	1983
275	365[a]	0.00	0.24	0.23	0.53	1984
275	365[a]	0.00	0.28	0.33	0.39	1985
275	365[a]	0.00	0.14	0.45	0.41	1986
275	365[a]	0.00	0.04	0.56	0.40	1987
275	365[a]	0.00	0.13	0.22	0.65	1988

[a]Values for each day in this simulation interval were estimated by linear interpolation between the tabled values for this interval and those of the preceding interval. For chinook salmon age 0+ and lake trout age 2+, data for intervals ending on day 365 of years 1982–88 are from day 1 of the next older age group (Tables 4 and 6).

1982–88

Simulations for each year from 1982 to 1988 were based on extensive new data from angler-caught salmonines taken between May and early September along western Lake Michigan (e.g. Hager 1984). We grouped data on diet composition of individual predator fishes by salmonine weights corresponding to age classes from Stewart et al. (1981, 1983) and then calculated an average diet composition for each month of each

TABLE 4. Proportional diet composition (P, by wet weight; subscripts are as given in Table 3) for Lake Michigan chinook salmon at various times of the year. Simulation day 1 is 1 May, and age 3+ of a simulation ends on day 214 when the salmon spawn and die. Estimates with corresponding sample sizes (n) are from angler-caught fishes along western Lake Michigan.

Simulation days		Food type											
		Age 1+				Age 2+				Age 3+			
Start	End	n	P_{OTH}	P_{SMA}	P_{LGA}	n	P_{OTH}	P_{SMA}	P_{LGA}	n	P_{OTH}	P_{SMA}	P_{LGA}
1982													
1	31	—[a]	0.30	0.32	0.38	—[a]	0.15	0.16	0.69	—[a]	0.14	0.11	0.75
32	61	—[a]	0.30	0.49	0.21	9	0.00	0.14	0.86	15	0.00	0.13	0.87
62	92	—[a]	0.47	0.36	0.17	54	0.70	0.36	0.57	40	0.05	0.24	0.71
93	123	19	0.21	0.36	0.43	60	0.15	0.14	0.71	35	0.07	0.21	0.72
124	365[a]	—[c]	0.15	0.16	0.69	—[d]	0.14	0.11	0.75	—[e]	0.07	0.21	0.72
1983													
1	31	—[f]	0.37	0.63	0.00	38	0.22	0.32	0.46	25	0.10	0.35	0.55
32	61	—[f]	0.14	0.86	0.00	22	0.07	0.43	0.50	15	0.08	0.21	0.71
62	92	—[f]	0.15	0.82	0.03	45	0.12	0.33	0.55	40	0.14	0.39	0.47
93	123	30	0.69	0.27	0.04	29	0.51	0.16	0.33	17	0.47	0.13	0.40
124	365[b]	—[c]	0.22	0.32	0.46	—[d]	0.10	0.35	0.55	—[e]	0.47	0.13	0.40
1984													
1	31	20	0.30	0.32	0.38	51	0.15	0.16	0.69	21	0.14	0.11	0.75
32	61	17	0.30	0.49	0.21	48	0.09	0.19	0.72	26	0.02	0.08	0.90
62	92	17	0.47	0.36	0.17	53	0.14	0.24	0.62	22	0.00	0.21	0.79
93	123	14	0.50	0.43	0.07	33	0.45	0.30	0.25	16	0.27	0.19	0.54
124	365[b]	—[c]	0.15	0.16	0.69	—[d]	0.14	0.11	0.75	—[e]	0.27	0.19	0.54
1985													
1	31	7	0.37	0.63	0.00	53	0.14	0.29	0.57	25	0.05	0.06	0.89
32	61	11	0.14	0.86	0.00	35	0.02	0.52	0.46	9	0.00	0.23	0.77
62	92	24	0.15	0.82	0.03	73	0.08	0.48	0.44	24	0.02	0.48	0.50
93	123	27	0.72	0.23	0.05	90	0.63	0.17	0.20	22	0.53	0.19	0.28
124	365[b]	—[c]	0.14	0.29	0.57	—[d]	0.05	0.06	0.89	—[e]	0.53	0.19	0.28
1986													
1	31	14	0.07	0.75	0.18	75	0.11	0.40	0.49	13	0.00	0.32	0.68
32	61	9	0.15	0.49	0.36	34	0.04	0.39	0.57	8	0.00	0.45	0.55
63	92	16	0.27	0.62	0.11	65	0.03	0.65	0.32	14	0.00	0.45	0.55
92	123	24	0.80	0.20	0.00	89	0.45	0.13	0.42	15	0.28	0.23	0.49
124	365[b]	—[c]	0.11	0.40	0.49	—[d]	0.00	0.32	0.68	—[e]	0.28	0.23	0.49
1987													
1	31	—[f]	0.37	0.63	0.00	8	0.00	0.18	0.82	—[f]	0.05	0.06	0.89
32	61	—[f]	0.14	0.86	0.00	13	0.08	0.79	0.13	—[f]	0.00	0.23	0.77
62	92	11	0.00	0.89	0.11	54	0.07	0.70	0.23	21	0.06	0.59	0.35
93	123	11	0.73	0.27	0.00	27	0.19	0.54	0.27	8	0.00	0.68	0.32
124	365[b]	—[c]	0.00	0.18	0.82	—[d]	0.05	0.06	0.89	—[e]	0.00	0.68	0.32
1988													
1	31	—[g]	0.07	0.75	0.18	—[g]	0.11	0.40	0.49	—[g]	0.00	0.32	0.68
32	61	—[g]	0.15	0.49	0.36	8	0.00	0.23	0.77	—[g]	0.00	0.45	0.55
62	92	15	0.02	0.60	0.18	31	0.01	0.40	0.59	9	0.00	0.48	0.52
93	123	13	0.55	0.27	0.08	23	0.13	0.48	0.35	4	0.00	0.82	0.18
124	365[b]	—[c]	0.11	0.40	0.49	—[d]	0.00	0.32	0.68	—[e]	0.00	0.82	0.18

[a]Data from 1984.
[b]Values for each day in this simulation interval were estimated by linear interpolation between the tabled values for this interval and those of the preceding interval.
[c]Data from day 1 of age 2+.
[d]Data from day 1 of age 3+.
[e]Data from day 123 of age 3+ applied through final day 214.
[f]Data from 1985.
[g]Data from 1986.

TABLE 5. Proportional diet composition (P, by wet weight; subscripts are as given in Table 3) for Lake Michigan coho salmon at various times of the year. Simulation day 1 is 1 April, and each simulation ends on day 244 when the salmon spawn and die. Estimates with corresponding sample sizes (n) are from angler-caught age 2+ fish from western Lake Michigan.

Simulation days		Food type				Food type		
Start	End	n	P_{OTH}	P_{SMA}	P_{LGA}	n	P_{OTH}	P_{SMA}	P_{LGA}
			1982				1983		
1	61	—[a]	0.04	0.31	0.65	46	0.40	0.28	0.32
62	91	51	0.04	0.31	0.65	27	0.11	0.51	0.38
92	123	22	0.10	0.23	0.67	26	0.13	0.22	0.65
124	244	38	0.06	0.14	0.80	6	0.56	0.06	0.38
			1984				1985		
1	61	105	0.25	0.32	0.43	156	0.17	0.59	0.24
62	91	106	0.24	0.35	0.41	132	0.05	0.44	0.51
92	123	103	0.19	0.18	0.63	122	0.07	0.45	0.48
124	244	—[b]	0.64	0.10	0.26	23	0.52	0.35	0.13
			1986				1987		
1	61	54	0.22	0.37	0.41	45	0.11	0.81	0.08
62	91	112	0.14	0.43	0.43	102	0.03	0.91	0.06
92	123	69	0.12	0.40	0.48	21	0.06	0.77	0.17
124	244	11	0.64	0.10	0.26	—[c]	0.52	0.35	0.13
			1988						
1	61	81	0.12	0.66	0.22				
62	91	54	0.15	0.57	0.28				
92	123	38	0.04	0.46	0.50				
124	244	10	0.10	0.35	0.55				

[a]Data from day 62 of 1982.
[b]Data from 1986.
[c]Data from 1985.

age group (Tables 4–6). In some cases (see below), it was necessary to pool data to minimize the number of small samples. The resulting diet tables represent our best effort to obtain a detailed assessment of temporal patterns without undue reliance on small samples. The sport harvest included few juvenile salmonines, so the diet data in Table 3 were used for 1982–88.

Chinook salmon diets were based on 2107 nonempty stomachs, with annual samples ranging from 103 to 620 fish (Table 4). A preliminary review of the data indicated that diets in 1983, 1985, and 1987 tended to be similar in having relatively lower proportions of large alewife. We therefore chose to fill in for missing or small samples by extrapolation between alternate years. For example, data from spring 1985 were used in place of small samples from spring 1987, and data from 1986 replaced some small samples from 1988 (Table 4). Winter diets were approximated by linear interpolation between the end of August (day 123) and 1 May of the next older age group. In most years, diets in August were more diverse than those for May–July (i.e. proportionately more fish other than alewife), perhaps due to seasonal offshore movements and recruitment of young for various species to the chinook salmon habitat. During winter, a diverse prey assemblage should become available as the lake cools and mixes.

Coho salmon diets were based on 1560 nonempty stomachs, with annual samples ranging from 105 to 433 (Table 5). We extrapolated data for May back to 1 April and data for August to the end of the spawning season (simulation day 244, 30 September). Missing data for May 1982 were extrapolated from June of that year. Missing or small samples from August 1984 and 1987 were filled in with data from 1986 and 1985, respectively, because of apparent similarities between patterns of other diet data for those alternate years.

Lake trout diets were based on 1135 nonempty stomachs, with annual samples ranging from 40 to 293 (Table 6). Because of the smaller samples and greater number of age classes, we had to pool data into only three weight groups (corresponding to ages 3–4, ages 5–6, and all larger fish). We further pooled data for May–July within each size group, but maintained the August data separate because they were typically the most distinctive. Alternate-year patterns of diet similarity were not evident for lake trout, so extrapolations were made as necessary from adjacent years or, in 1987, from a larger size class.

Relative Predation

To compare relative predatory impact of coho and chinook salmon and lake trout under various conditions, we ran simulations for each species starting with 1 million fish in each case as in Stewart et al. (1981). Results for each species represent the annual predation by the population that would result from many years of stocking exactly 1 million fingerlings each year. Results also represent the effect of stocking 1 million fish and summing their consumption until they have all died. For each of the three species, we ran one simulation representing typical conditions for the years 1978–81. To represent conditions after the 1981–83 alewife decline, we averaged diet and predator weight data across years. For coho salmon, we ran one simulation with diet and weights typical of 1984, 1986, and 1988 and another simulation for conditions typical of 1983, 1985, and 1987. For chinook salmon, we averaged diet and predator weights for 1984–88, and for lake trout, we averaged diets only for 1983–88.

Moreover, two possible future scenarios were simulated. In the first one, we assumed that chinook salmon would feed exclusively on bloater, now the most abundant species in Lake Michigan. Bloater live in relatively deep water, so the maximum summer temperature for chinook would be about 8°C (Brandt et al. 1991) versus 11°C in our nominal simulations. For this simulation, we used the same ration (P, proportion of maximum possible) as for our 1987 nominal simulation, but the lower temperature reduced consumption and growth potential. In the second hypothetical scenario, we assumed that survival of lake trout increased from 52 to 60% after age 4, in accordance with existing management goals (Rybicki 1983).

Modeling Results and Discussion

Diet Composition

Integration of the available diet information through modeling simulations for each year reveals some striking patterns (Fig. 4). Diets of coho and chinook salmon shifted from heavy reliance on large alewife in the late 1970's to more equal utilization of large alewife, small alewife, and other fishes in the mid-1980's. From 1984 to 1986, fish other than alewife increased in the diet, but in 1987 and 1988, the Pacific salmon substituted juvenile alewife for other fish in their diet. In 1987–88, total alewife in their diets was similar to the 1970's, but relative percentage of large alewife in the diet has remained at

TABLE 6. Proportional diet composition (P, by wet weight; subscripts are as given in Table 3) for Lake Michigan lake trout at various times of the year. Simulation day 1 is 1 July. Estimates with corresponding sample sizes (n) are from angler-caught fishes from western Lake Michigan. Winter data for days 168 and 274 (Eck and Wells 1986) were applied to all years from 1978 to 1988 because they were the only winter data available to us. In each year from 1982 to 1988, data for days 1–31 (July) were the same as those for days 305–365 (May and June) because estimates are of pooled data for those three months. See values for 1982 for an example.

Simulation days		Food type											
		Ages 3+ and 4+				Ages 5+ and 6+				Ages 7+ to 9+			
Start	End	n	P_{OTH}	P_{SMA}	P_{LGA}	n	P_{OTH}	P_{SMA}	P_{LGA}	n	P_{OTH}	P_{SMA}	P_{LGA}
1982													
1	31	22	0.31	0.07	0.62	15	0.20	0.09	0.71	10	0.12	0.09	0.79
32	62	24	0.33	0.33	0.64	15	0.47	0.00	0.53	—[a]	0.52	0.00	0.48
63	168[b]	—[c]	0.12	0.84	0.04	—[d]	0.48	0.02	0.50	—[f]	0.17	0.54	0.29
		—[e]	0.30	0.60	0.10	—[f]	0.17	0.54	0.29				
169	274[b]	—[c]	0.99	0.01	0.00	—[d]	0.73	0.00	0.27	—[f]	0.66	0.00	0.34
		—[e]	0.82	0.00	0.18	—[f]	0.66	0.00	0.34				
275	305[b]	—[g]	0.31	0.07	0.62	—[g]	0.20	0.09	0.71	—[g]	0.12	0.09	0.79
306	365	—[g]	0.31	0.07	0.62	—[g]	0.20	0.09	0.71	—[g]	0.12	0.09	0.79
1983													
1	31	86	0.31	0.19	0.50	86	0.22	0.06	0.72	29	0.05	0.11	0.84
32	62	36	0.55	0.03	0.42	37	0.45	0.00	0.55	19	0.52	0.00	0.48
1984													
1	31	59	0.24	0.23	0.53	80	0.22	0.15	0.63	46	0.21	0.13	0.66
32	62	15	0.65	0.07	0.28	38	0.52	0.06	0.42	33	0.52	0.01	0.47
1985													
1	31	47	0.28	0.33	0.39	34	0.20	0.27	0.53	41	0.17	0.20	0.63
32	62	15	0.61	0.08	0.31	15	0.50	0.03	0.47	27	0.75	0.00	0.25
1986													
1	31	35	0.14	0.45	0.41	34	0.11	0.25	0.64	53	0.07	0.16	0.77
32	62	12	0.60	0.10	0.30	12	0.51	0.04	0.45	12	0.50	0.08	0.42
1987													
1	31	27	0.04	0.56	0.40	34	0.02	0.33	0.65	30	0.04	0.35	0.61
32	62	—[h]	0.43	0.00	0.57	8	0.43	0.00	0.57	9	0.68	0.06	0.26
1988													
1	31	11	0.13	0.22	0.65	16	0.01	0.31	0.68	13	0.00	0.17	0.87
32	62	—[i]	0.43	0.00	0.57	—[i]	0.43	0.00	0.57	—[i]	0.68	0.06	0.26

[a]Data from 1983.
[b]Values for each day in this simulation interval were estimated by linear interpolation between the tabled values for this interval and those of the preceding interval.
[c]Data for age 3+ from Eck and Wells (1986).
[d]Data for age 5+ from Eck and Wells (1986).
[e]Data for age 4+ from Eck and Wells (1986).
[f]Data for age 6+ from Eck and Wells (1986).
[g]Data same as days 1–31 for these ages.
[h]Data from ages 5+ and 6+ for 1987.
[i]Data from 1987 for these ages.

about 30–40% since 1983. Our results for 1987–88 suggest possible strong year classes of alewife in 1986 and 1987. Diets of lake trout have remained relatively stable throughout this period (Fig. 4). Prior to 1983, lake trout generally had a more diverse diet with less reliance on large alewife than the Pacific salmon (Stewart et al. 1981, 1983; Eck and Brown 1985; Jude et al. 1987).

Relative Predation Rates

The temporal trends illustrated in Fig. 4 were influenced, in part, by year-to-year changes in population age structure. To control that variable and to allow a more equitable comparison among species, we ran simulations for a standard 1 million individuals under various conditions (Fig. 5). Comparing results of our simulations for 1978–81 with those of Stewart et al. (1981) reveals only minor differences for coho and chinook salmon, but a 47% decline in relative predation by the lake trout population (Fig. 5). Decline in the modeled lake trout predation was due largely to changes in growth and mortality assumptions based on Eck and Brown (1985). If growth did not decline in the central and northern parts of the lake (Keller et al. 1989), then our estimates for lake trout predation would be low.

Lake Michigan coho salmon showed an interesting oscillation in average weight in the sport catch, being about 18% smaller in 1984, 1986, and 1988 compared with 1983, 1985, and 1987. Similar variation may also have been occurring in the 1970's (Hansen 1986). Comparing results of simulations

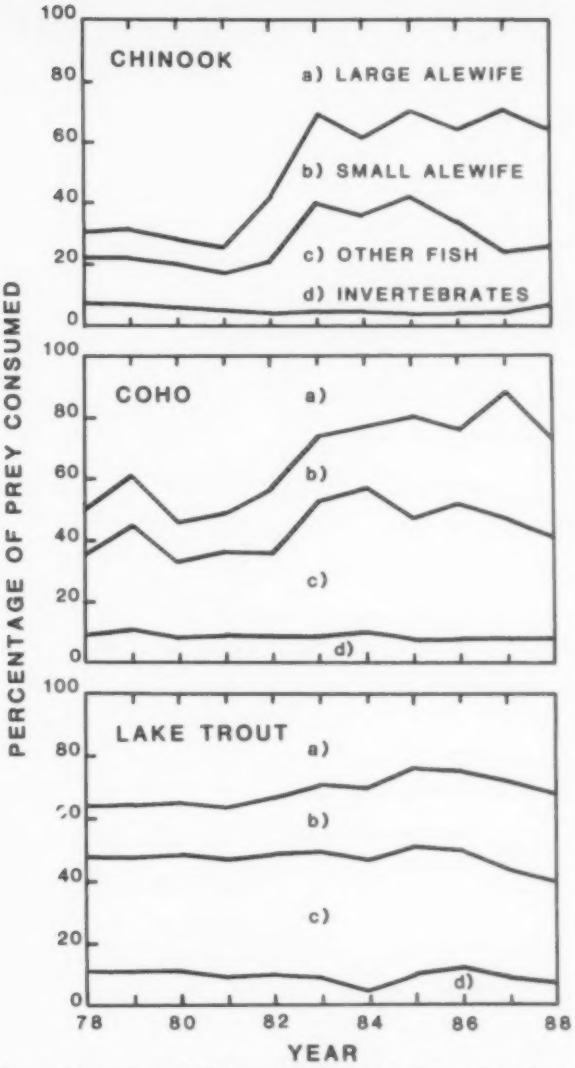

FIG. 4. Comparison of diet composition for lake trout, coho salmon, and chinook salmon populations in Lake Michigan based on modeling simulations of predation for each year from 1978 to 1988. Large and small alewife are greater than and smaller than 8 g wet weight.

for average conditions in each of those sets of years indicates that diets in good growth years may be supplemented with juvenile alewife. We infer from this that there may be a previously unrecognized 2-yr cycle in success of juvenile alewife in Lake Michigan. It is possible that standard bottom trawl surveys do not effectively sample young-of-year and yearling alewife (Hatch et al. 1981; Eck and Brown 1985). Similar short-term responses of salmonine growth to abundances of young alewife have been observed for coho salmon and brown trout in Lake Ontario (O'Gorman et al. 1987).

Total predation per million chinook salmon declined about 8% after the alewife decline in 1981–83 and the resulting diet shift away from large alewife (Fig. 5). Weight of the average individual chinook salmon in the sport catch for 1984–88 averaged 24% lower than 1982, reflecting lower conversion efficiency for the changed diet (see below). We infer that growth of chinook salmon in Lake Michigan was limited by quantity and quality of available forage, at least during 1984–86 and 1988. Our hypothetical scenario for chinook salmon feeding on bloater suggested that we might see further declines of consumption (−23%) and mean individual weight (−16 to −19%) under those conditions. These estimated reductions are entirely temperature effects because ration as a proportion of maximum and average energy density of the diet were held constant. If salmon have more difficulty catching bloater than they do catching alewife, then rations might also decline, leading to even more extreme growth declines. That could happen, for example, because bloater attain a larger size than alewife and generally inhabit deeper strata where low light levels might restrict a salmon's ability to find prey.

Predation per million lake trout showed little effect from the 1981–83 alewife decline. Likewise, increasing the annual survival rate of lake trout to 60% after age 4 (when they enter the sport fishery) increased forage demand only 10%. Predation estimates for lake trout were much more sensitive to changes in survival rates of the juveniles than to changes in adult survival rates. Management efforts to reduce incidental catch of juvenile lake trout (e.g. Keller et al. 1989) thus may influence predation pressure on prey fish stocks more than regulations to limit removal of adult fishes.

Total Salmonine Predation

Total salmonine predation by stocked fishes increased from about 44 000 t in 1978 to a peak of about 71 000 t in 1983, declined, and then peaked again at 76 000 t in 1987 (Fig. 6A). The first peak coincided with the years of greatest alewife decline (1981–83). That decline, however, was preceded by a series of severe winters that may have been its primary cause (Eck and Brown 1985), or at least would have compounded the predation effects. Total predation by chinook salmon doubled between 1978 and 1983, while that by coho salmon and lake trout (excluding the deep reef fishes) declined. Over the 11-yr period, stocked rainbow and brown trout may have contributed 15–31% annually to the overall predation pressure. Total salmonines stocked peaked about 1984 and has declined slightly since then (Table 2), in part because of management concern for stability of the alewife population. The secondary peak of predation effects in 1987 may partially reflect maturing of the fishes stocked in 1984. It also reflects larger average weight of chinook salmon in the 1987 sport catch compared with weights in 1984–86 and 1988.

Composition of total prey biomass consumed by the three modeled salmonines (Fig. 6B) strongly mirrors diet composition of the chinook salmon (Fig. 4) because they account for a large proportion of that total. Between 1982 and 1983, consumption of large alewife decreased from 28 580 to 16 350 t and remained around that level through 1988. Predation on small alewife oscillated between 10 000 and 16 000 t since 1982, except for a peak of 25 000 t in 1987. Consumption of prey fish other than alewife almost doubled from 11 390 t in 1982 to 20 500 t in 1983 and then gradually declined to 10 000 t in 1988. Predation on fishes other than alewife fell heaviest on rainbow smelt (*Osmerus mordax*), with juvenile yellow perch (*Perca flavescens*), juvenile bloater, and slimy sculpin (*Cottus cognatus*) of secondary importance.

Conversion Efficiency

The effects of diet changes and slower growth resulted in about a 20% decline in wet weight gross conversion efficiency

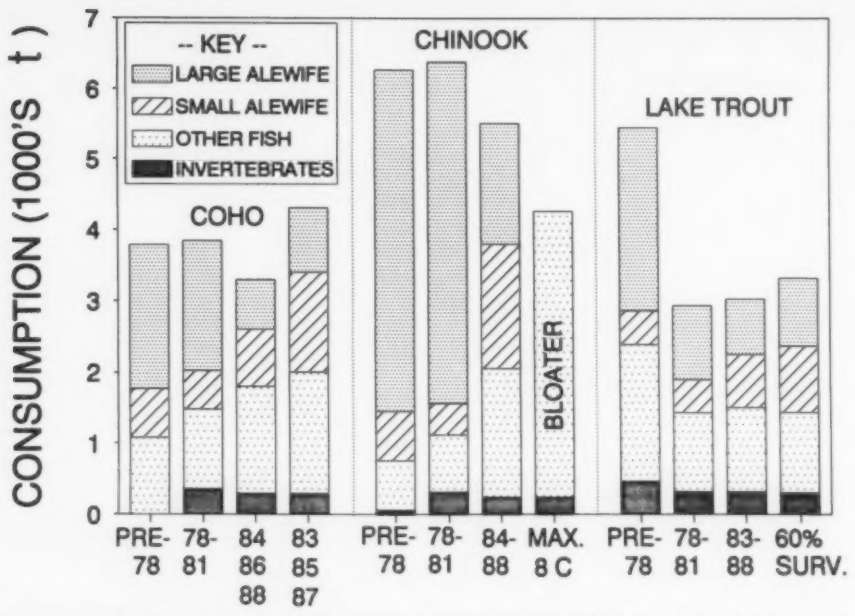

FIG. 5. Comparison of total consumption and breakdown by prey type for a standard 1 million stocked fish for each of coho salmon, chinook salmon, and lake trout in Lake Michigan. Results from Stewart et al. (1981) are presented as Pre-78, and those simulations were adjusted for 1978–81 by including results from Jude et al. (1987; cohort 1 diets for coho and chinook salmon), Eck and Brown (1985; lake trout growth and survival rates), and Eck and Wells (1986; lake trout winter diets). Results for the period after the main alewife decline (1983–88) are based on average growth and diets for the years indicated above each bar (see text). We also present results of two hypothetical scenarios involving chinook salmon eating bloater at 8°C and lake trout with 60% annual survival after age 4.

for chinook salmon since the late 1970's (Fig. 7). Much of that decline stems from eating less of the energy-rich large alewife and more prey of lower energy content. Lower efficiency means that the chinook have to increase their daily ration to accomplish the same growth rates that they previously attained. If they are not able to increase their rations, then growth would slow down. The decline in mean weight of chinook salmon in the sport catch since 1982 may be indicative of such a problem. The alternating fast- and slow-growth years of coho salmon and associated diet changes are also reflected in a slight interannual oscillation in conversion efficiency. Efficiency was lower in 1985 and especially in 1987 when small alewife became more important in the diet at the expense of larger alewife. Conversion by lake trout was relatively stable over the study period.

Total Salmonine Production

Total gross production for the three modeled salmonines has remained relatively stable near 10 000 to 11 000 t since 1980 (Fig. 8). That is because early-summer total population for those three species combined was reasonably stable between 17 and 19 million fishes from 1979 to 1987 (Table 2). As with predation, chinook salmon have accounted for over half the salmonine production since the early 1980's. Total lakewide gross production by all stocked salmonines was estimated to be about 15 300 t in 1987, or 0.27 $g \cdot m^{-2}$ of lake surface. That amount of production is similar to historic levels of commercial yields of all fishes in Lake Michigan (Leach et al. 1987, table 3, 0.22 $g \cdot m^{-2}$).

Ratios of gross annual production to mean monthly population biomass in 1987 were calculated for each of the three modeled salmonines (Fig. 8). That ratio was clearly highest for chinook salmon (1.6), intermediate for coho salmon (1.15), and lowest for lake trout (0.6). Those striking differences between species further explain why chinook salmon are so popular with fishery managers in the Great Lakes. Values for coho and chinook salmon are typical of those for salmonine populations from relatively cold streams, but the production to mean biomass ratio for lake trout is noticeably lower than for most populations of stream salmonines (Chapman 1978).

Discussion

Predator–Prey Dynamics

The foregoing results indicate a strong preference for large alewife by Lake Michigan salmonines. If large alewife become scarce, salmonines switch progressively to immature alewife and finally to rainbow smelt and other prey fishes. Implications are that growth of Pacific salmon (as reflected in average size of sport-caught fishes) is very responsive to short-term changes in abundance of alewife. Our predation estimates based on average size in the sport catch may be lower than actual for chinook salmon because we assumed that most lived no longer than 4 yr. There is now evidence that some chinook may be living to 5 or 6 yr (M. Toneys, Wisconsin Department of Natural Resources, Sturgeon Bay, WI, and R. Hay, Michigan Department of Natural Resources, Cadillac, MI, pers. comm.), but we no not know if that applies to the entire population or only those runs that have been studied. If they are now taking more years to attain weights similar to those modeled here, then

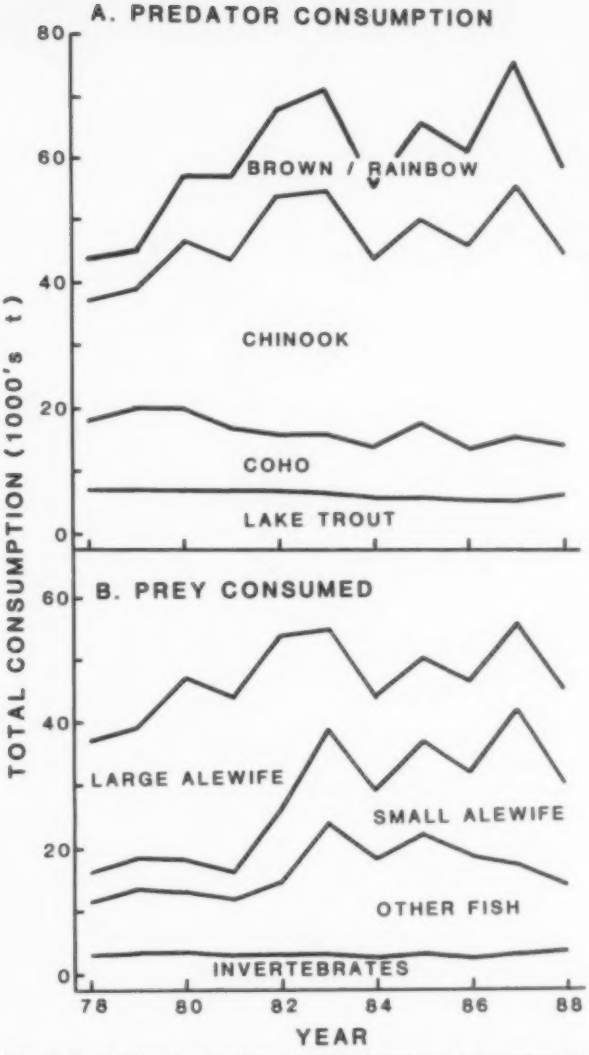

FIG. 6. Total salmonine predation in Lake Michigan during 1978–88 based on modeling simulations of lake trout, coho salmon, and chinook salmon. (A) Broken down by predator species and extrapolated to include rainbow and brown trout by assuming that whole population predation per yearling stocked (including yearling equivalents of previous year's fall fingerlings) was comparable as the average of that for the three species simulated; (B) broken down by prey type for the three species simulated.

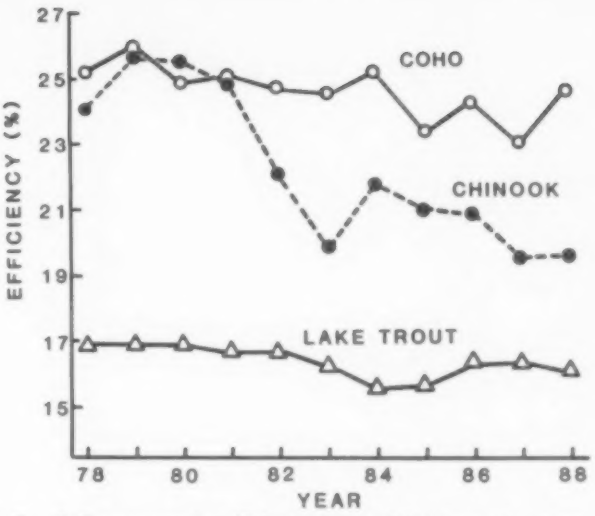

FIG. 7. Gross conversion efficiency of wet weight biomass (i.e. cumulative gross production divided by total consumption) for lake trout, coho salmon, and chinook salmon populations in Lake Michigan based on modeling simulations for 1978–88.

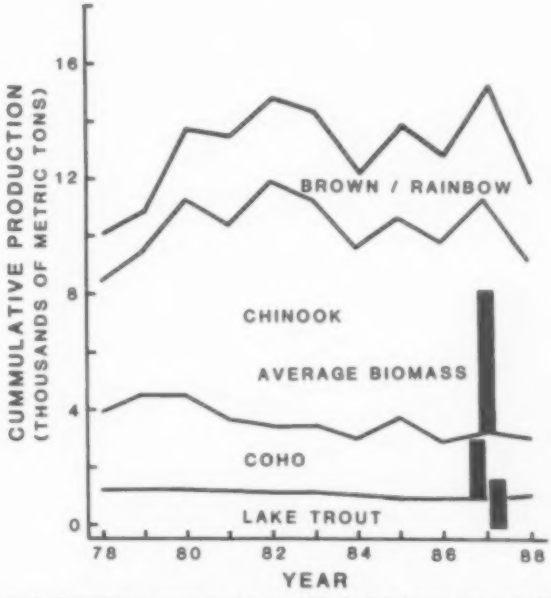

FIG. 8. Cumulative gross production in Lake Michigan during 1978–88 based on modeling simulations of lake trout, coho salmon, and chinook salmon. We extrapolated to rainbow and brown trout assuming that whole population production per yearling stocked (including yearling equivalents of previous-year's fall fingerlings) was comparable with the average per individual stocked for the three species simulated. Vertical bars for 1987 indicate the average population biomass on the last day of each calendar month for the three species simulated, providing a comparison of production to biomass ratios.

consumption estimates would be higher and conversion efficiency lower than our estimates. If salmon continue their strong preference for large alewife as that population declines, we may see a progressive deterioration of the alewife reproductive stock. Such a process could partially explain failure of the alewife population to recover after the decline in 1981–83.

Prior to 1982, the alewife population showed wide fluctuations from year to year and the population would recover quickly after a sharp decline (Eck and Wells 1987). That pattern is still evident for the Lake Ontario alewife population (O'Gorman et al. 1987), but the Lake Michigan population appears to have lost that capacity to rebound quickly. Before 1982, alewife population dynamics may have been dominated by intraspecific and physical (weather) processes. Subsequently, the interspecific interactions such as heavy predation by salmonines may have become the dominant forces regulating the alewife population.

Less extreme year-to-year variations of alewife population abundance and reasonable growth of salmonines (by Pacific Ocean standards) suggested that managers of the system might be able to "have their cake and eat it too," that is, a reduced alewife population that allows rehabilitation of native fishes, but enough alewife to feed the salmonines. We should not be lulled into a false sense of security by 6 yr of apparently stable alewife populations, however, because stability of the present prey–fish assemblage remains to be tested by a harsh winter. Severely cold winters in 1976–77 and 1983–84 reduced alewife populations in both Lakes Michigan and Ontario (Eck and Wells 1987; O'Gorman et al. 1987). There has not been such a severe winter in the past 6 yr. When (not if) the next one occurs, it will provide a critical test for alewife in both lakes. Conceivably, Lake Michigan alewife may be in good condition by virtue of their smaller population and presumably lowered intraspecific competition. If that is the case, then they may be more resistant to drastic mortality from an extreme winter (O'Gorman et al. 1987). If mortality from cold stress (Colby 1973) can occur relatively independent of condition, or if food limitations prevent enhanced condition of the alewife, then the next severe winter could mean further decline in their population. There is no historical precedent from which to predict the outcome. Dramatic surprises are possible.

Further declines in alewife could yield still smaller Pacific salmon in the sport catch. Lowered scope for growth at the low temperatures required to forage on bloater and rainbow smelt, and perhaps also at higher temperatures required to feed effectively on yellow perch, could limit size of salmon in the fishery. If prey alternatives to alewife are not sufficiently abundant when and where the salmon need them, slower growth could translate into stress, disease, and mortality. Lower survival of salmon may be the ultimate stabilizing force in Great Lakes ecosystems that will prevent complete elimination of alewife.

Returns of spawning chinook salmon to certain streams in Michigan began to decline about 1985, and by 1988 may have been 40–50% lower than in the early 1980's (R. Hay, Michigan Department of Natural Resources, Cadillac, MI, pers. comm.). Die-offs of large chinook salmon in southern Lake Michigan have occurred in the springs of 1988–90, with the ultimate cause of death apparently being bacterial kidney disease (D. Brazo, Indiana Department of Natural Resources, Michigan City, IN, pers. comm.). Total sport harvest of chinook salmon from Lake Michigan has also declined in the past 2 yr (Keller et al. 1989), but that change is confounded by reduced fishing effort by anglers who heard reports of lower catch rates. Lower catch rates might, in turn, reflect a change of foraging behavior by the salmon as they seek alternative prey. In short, chinook salmon survival rate may have recently declined by up to 50%, but we did not model that change because of the foregoing uncertainties about the actual lakewide values. If available evidence is indicative of lakewide conditions, then our predation and production estimates for chinook salmon in 1987 and 1988 may need to be lowered appropriately. This possible bias towards a high predation estimate for chinook may be balanced, however, by possible low biases from our assumptions about lake trout growth, and by not including naturally spawned salmonines in this analysis.

Implications for Management and Future Research

Comparison of our predation estimates, commercial landings, and available production of alewife in Lake Michigan indicates that about 60% of that production is now being "harvested" annually (Brandt et al. 1991). The system probably cannot support a marked increase in alewife harvests. Keller et al. (1989) have suggested that further increases in stocking of salmonines may be possible because of the large biomass of bloater in the lake. That may be a fair assessment for lake trout that historically fed on bloater (Van Oosten and Deason 1938; Eck and Brown 1985), but our results suggest that increases in Pacific salmon densities will affect alewife first and foremost. Even lake trout stocked in shallow water appear to prefer alewife when they are available. We believe that a goal of increasing stocking densities for Pacific salmon to take advantage of available bloater production (Keller et al. 1989) is in direct conflict with one of maintaining alewife as an important prey in the system.

While we suggest possible incompatibilities among certain management goals of Keller et al. (1989), we agree entirely with their perceived research needs. Uncertainties in the present analysis derive in part from incomplete information on age-specific growth and survival rates, especially for the juvenile salmonines. Those are clearly research topics that beg additional expenditure of field efforts. The cost of research to understand early life history processes in juvenile salmonines would certainly be much less than one year's loss of economic returns to communities of the Lake Michigan basin that have suffered from the recent decline of salmonine catch rates. We have also omitted consideration of naturally spawned salmonines because lakewide data are inadequate.

Natural processes may have perturbed the Lake Michigan system by reducing salmonine predation to a much lower level than managers could possibly have done in today's sociopolitical climate. If so, we should take full advantage of that natural experiment to further our understanding of predator–prey dynamics in the Lake Michigan system. We should also be prepared to make appropriate observations on alewife when the next harsh winter arrives because that will be the acid test of stability for their population. Finally, we believe that important insights can be gained from between-lake comparisons (e.g. Leach et al. 1987), but so far, estimates of whole-lake salmonine predation and prey–fish production are lacking for the four Great Lakes along the U.S.–Canadian border.

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Bacterioplankton Density and Activity in Benthic Nepheloid Layers of Lake Michigan and Lake Superior[1]

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Hicks, R. E., and C. J. Owen. 1991. Bacterioplankton density and activity in benthic nepheloid layers of Lake Michigan and Lake Superior. Can. J. Fish. Aquat. Sci. 48: 923–932.

Benthic nepheloid layers were observed in Lake Michigan and Lake Superior during July 1988 using the *Johnson-Sea-Link II* submersible. A particularly well-defined benthic nepheloid layer was present in Whitefish Bay, Lake Superior, where particle concentrations increased 10 times over the bottom 30 m. Bacterial abundance, however, increased only 1.5 times in the same depth interval and a maximum of only 16% 1 m above the sediment in both lakes when the sediment boundary layer was deliberately resuspended. Bacterial abundance was greater in Lake Michigan than in Lake Superior. Bacterioplankton abundance and the frequency of dividing cells were both related to temperature and organic carbon concentrations. The range of individual cell volumes (0.024–0.042 μm^3) was similar in both lakes, regardless of depth. Less than 5% of the heterotrophic bacteria were actively dividing and only 2.0–3.4% of the bacterioplankton in the epilimnion and hypolimnion were synthetically active in both lakes. Bacterioplankton doubling times, estimated from field measurements of the frequency of dividing cells, increased from 29 h at 5 m to >230 h at 310 m in the Caribou Basin of Lake Superior. The abundance, cell size, and activity of heterotrophic bacterioplankton in the deep hypolimnia of Lake Michigan and Lake Superior were unaffected by the presence of a benthic nepheloid layer.

Des couches benthiques néphéloïdes ont été observées dans les lacs Michigan et Supérieur en juillet 1988 à l'aide du submersible *Johnson-Sea-Link II*. L'une d'elle, dans la baie Whitefish dans le lac Supérieur, était particulièrement bien définie : les concentrations des particules s'y accroissaient d'un facteur 10 dans les 30 m au-dessus du fond. Dans le même intervalle de profondeur, cependant, l'abondance des bactéries ne s'accroissait que de 1,5 fois et d'au plus 16 % dans le premier mètre au-dessus du fond, dans les deux lacs, quand les sédiments du fond étaient délibérément resuspendus. Les bactéries étaient plus abondantes dans le lac Michigan que dans le lac Supérieur. L'abondance du bactérioplancton et le taux de division cellulaire étaient tous deux fonction de la température et des concentrations en carbone organique. Le volume des cellules (0,024 à 0,042 μm^3) était similaire dans les deux lacs, quelle que soit la profondeur. Moins de 5 % des bactéries hétérotrophes se divisaient activement et seulement 2,0 à 3,4 % du bactérioplancton de l'épilimnion et de l'hypolimnion montrait une activité synthétique dans les deux lacs. Le temps de doublement du bactérioplancton, estimé à partir de mesures, prises sur place, de la fréquence des divisions cellulaires, passait de 29 h, à 5 m, à plus de 230 h à 310 m dans le bassin Caribou, au lac Supérieur. La présence de couches benthiques néphéloïdes dans les lacs Michigan et Supérieur n'avait pas d'effet sur l'abondance, la taille et l'activité du bactérioplancton hétérotrophe de l'hypolimnion profond.

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The benthic nepheloid layer (BNL) is a zone above the sediment where small particles (2–8 μm) concentrate after the water column becomes thermally stratified. It is a prominent feature of marine systems and the Laurentian Great Lakes (Chambers and Eadie 1981; Gardiner and Sullivan 1981; McCave 1983; Sandilands and Mudroch 1983). This optically distinct layer usually extends 5–30 m above the sediment during the summer in Lake Michigan and Lake Superior, but it may, at times, extend to the top of the hypolimnion in Lake Michigan due to the lake's seiche and oscillating thermocline (Eadie et al. 1983; Eisenreich 1987; Halfman and Johnson 1989). This expanded BNL has been called a bottom turbid layer (Chambers and Eadie 1981). Organic particles from surface waters and resuspended sediment eventually settle through the BNL to form a fluffy layer, about 5 mm deep, at the sediment surface called the sediment boundary layer (SBL). The BNL and SBL together have been referred to as the benthic boundary layer and we will adhere to this usage (Eadie et al. 1983). They have received less attention than other parts of the water column or sediments and data remain scarce about the character and microbiology of these zones in Laurentian Great Lakes. The objective of this study was to measure the density of bacteria, their cell volume, the frequency of dividing cells (FDC), and the frequency of synthetically active bacteria (SAB) in microbial communities within the BNL and SBL and compare them with the epilimnion communities of Lake Michigan and Lake Superior.

Fast-sinking particles (>1 $m \cdot d^{-1}$) and aggregates produced in the epilimnia of the Great Lakes rapidly transport organic matter and contaminants to benthic regions (Eadie et al. 1984). This organic matter is partially degraded before being buried in sediments. In Lake Superior, the amount of organic matter degraded in the BNL is greater than in other parts of the water

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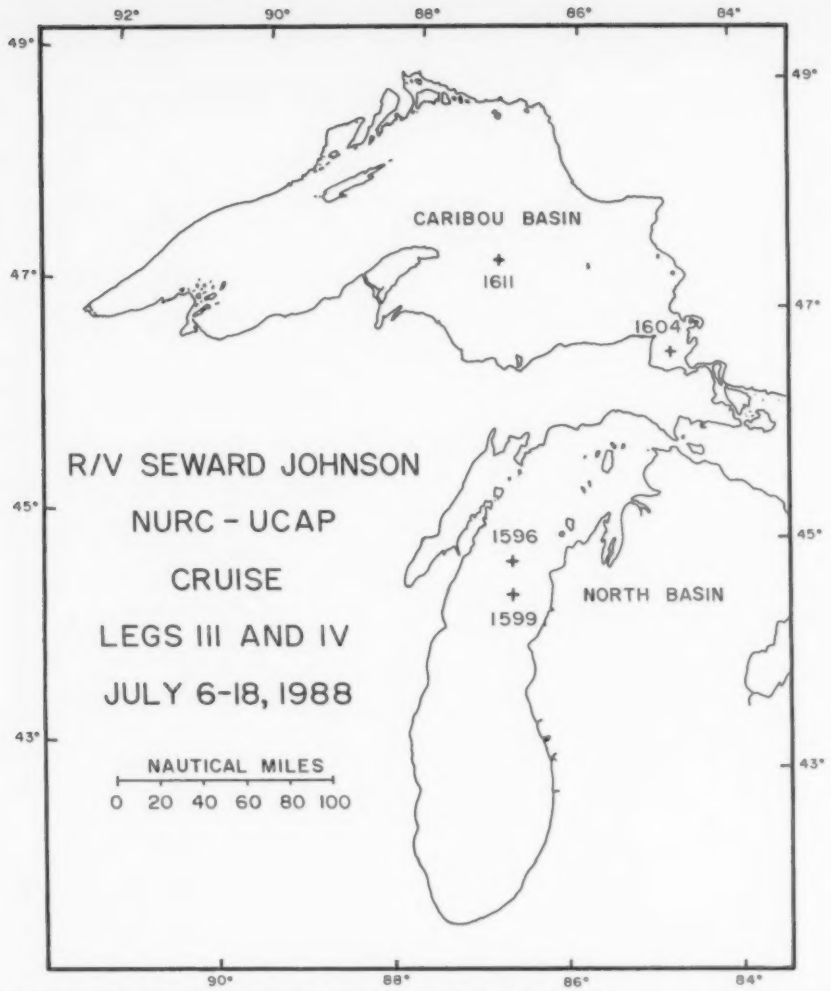

FIG. 1. Location of dive sites in Lake Michigan and Lake Superior. Data are presented from four submersible dives in the North Basin (dives 1596 and 1599), Whitefish Bay (dive 1604), and the Caribou Basin (dive 1611) during July 1988.

column and the degradation rate of organic matter in the BNL is thought to be much faster than the rate in the underlying sediment (Baker and Eisenreich 1989). The mineralization of organic matter and subsequent release of adsorbed polychlorinated biphenyls (PCBs) may be responsible for the increased concentrations of dissolved PCBs observed in the BNL of Lake Superior (Eisenreich 1987).

Sediment resuspension by benthic organisms, seiches, currents, storms, and periodic lake turnover contributes to the maintenance of BNLs (Rhoads et al. 1984; Bedford and Abdelrhman 1987). Klump et al. (1980) demonstrated that 15–40% of the organic carbon deposited to sediments to Lake Superior is returned to the water. Resuspended sediments may replenish dissolved organic carbon (DOC) in addition to returning particulate organic carbon (POC) to the water column. This recycled DOC has been suggested to support more bacterial production in the epilimnion during the summer than can be accounted for by new primary production alone (Scavia and Laird 1987; Scavia 1988).

Only a few percent of the POC and less than 1% of the PCBs reaching the bottom waters accumulate in the sediments (Baker et al. 1985; Baker and Eisenreich 1989). This large loss of organic matter in the BNL may be caused by greater bacterioplankton density or by greater cell activity in this zone. Many heterotrophic bacteria in aquatic environments, however, are not metabolically active, even in systems more productive than the Great Lakes (Roszak and Colwell 1987). Several factors may control the activity of heterotrophic bacteria in the BNL, including oxygen availability, the concentration and composition of suitable organic substrates, and temperature. Anaerobic conditions rarely develop above 0.8 cm in the sediments of Lake Superior and oxygen-supported respiration accounts for 94% of the carbon metabolism in these sediments (Carlton et al. 1989). Bacterial production in aerobic zones is significantly correlated with plankton primary production and the release of DOC by phytoplankton (Cole et al. 1988). Production by heterotrophic bacteria, however, can also be tightly coupled to seasonal or habitat differences in temperature (Pomeroy and Deibel 1986). Our goal was to determine if the abundance or

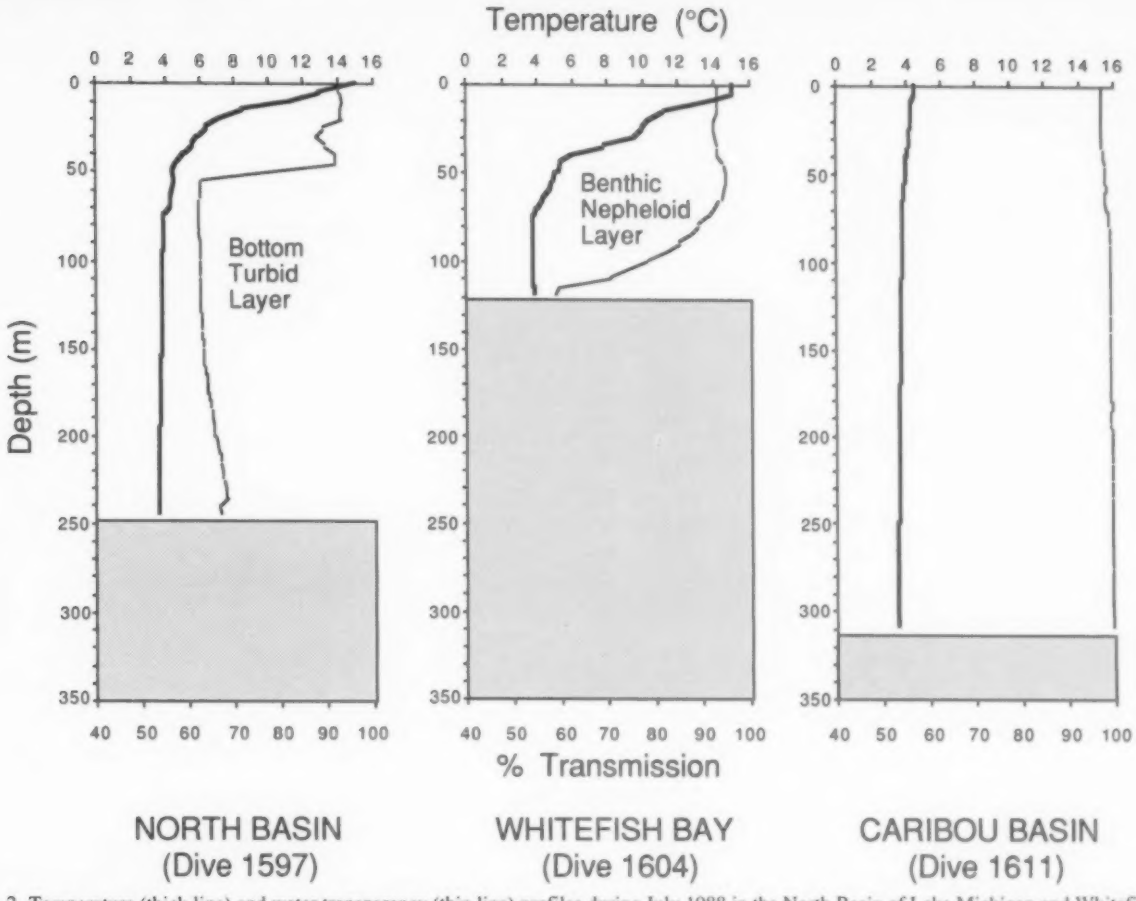
Temperature (°C)
0 2 4 6 8 10 12 14 16
Depth (m)
0 50 100 150 200 250 300 350
Bottom Turbid Layer
Benthic Nepheloid Layer
40 50 60 70 80 90 100
% Transmission
NORTH BASIN (Dive 1597)
WHITEFISH BAY (Dive 1604)
CARIBOU BASIN (Dive 1611)

FIG. 2. Temperature (thick line) and water transparency (thin line) profiles during July 1988 in the North Basin of Lake Michigan and Whitefish Bay and the Caribou Basin of Lake Superior. Note the high water clarity and absence of a turbid zone at the Caribou Basin site.

activity of heterotrophic bacterioplankton increases when the temperature, POC, and DOC concentrations in the deep hypolimnia of Lake Michigan and Lake Superior are encountered which would help explain the large losses of organic compounds in this zone.

Methods

Study Sites

Samples were collected aboard the R/V *Seward Johnson* and the *Johnson-Sea-Link II* (*JSL-II*) research submersible (Harbor Branch Oceanographic Institution, Inc., Fort Pierce, FL) on July 6–18, 1988. Two sites in the North Basin of Lake Michigan were sampled (dives 1596 and 1597, 44°46.04′N, 86°42.98′W; dive 1599, 44°28.94′N, 86°42.93′W). Two sites, Whitefish Bay (dive 1604, 46°45.02′N, 84°46.97′W) and the Caribou Basin (dive 1611, 47°22.17′N, 86°57.99′W), were visited in Lake Superior (Fig. 1). Water temperature and transparency were measured as the *JSL-II* descended to the bottom of these lakes with a Sea-Bird CTD/Sea-Tech transmissometer (25-cm pathlength) system attached to the submersible.

Sample Collection

Surface water (5 and 25 m) was collected from the ship using a submersible pump (March Mfg., Glenview, IL, model 5C-MD) attached to 2.5-cm-diameter Tygon tubing (Baker et al. 1985). This system was flushed for several minutes before taking a sample. Water samples from below 25 m were taken through a 3-mm-diameter Tygon tube (dead volume ≈ 79 mL) connected to the submersible robotic arm using the pressure difference between the water and the submersible dive chamber at each depth (McKee et al. 1989). At least 250 mL of water was flushed through this tubing before samples were taken. The robotic arm of the *JSL-II* was used to resuspend the SBL after sampling bottom water (1 m above sediment; BNL) to determine if sediment resuspension would significantly increase the density of bacterioplankton, the FDC, or the number of synthetically active bacteria in the BNL water. Three independent water samples (replicates) were collected at 5 m, in the middle of the water column, and 1 m above the sediment surface before and after deliberately resuspending the SBL. Only one water sample was collected at other depths in the water column, except at the Whitefish Bay site where three samples were collected. All water samples were collected in acid-washed polypropylene or glass bottles that had been rinsed with 0.2-μm-filtered distilled water. Samples were processed less than 30 min after sampling.

After subsamples were removed for bacterial counts, the remaining water (0.5–2.0 L) was filtered through preweighed,

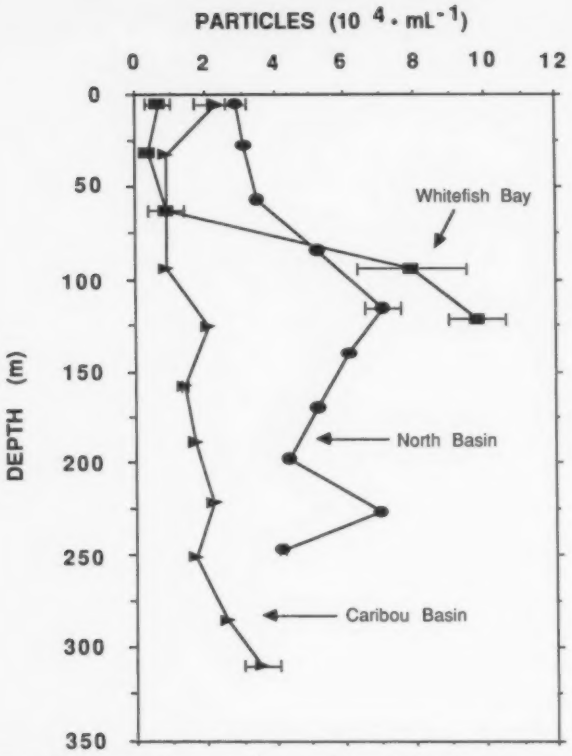

FIG. 3. Concentration of small suspended particles (diameter range 0.2–2.5 μm) in the water column of Lake Michigan (North Basin) and Lake Superior. Nonliving particles were counted using epifluorescence microscopy after DAPI staining. Bars denote the standard error of the mean when replicate water samples were taken (n = 3).

ashed, glass fiber filters (Gelman A/E). Filters were stored frozen. They were dried at 100°C for 24 h and reweighed to measure suspended solids. Separate water samples for POC and DOC analyses were collected at 5, 25, and 1 m above the sediment. POC collected on duplicate glass fiber filters and in duplicate sediment core sections was measured using a dichromate wet oxidation method (Parsons et al. 1984; Baker and Eisenreich 1989). Inorganic carbon was not measured; it does not interfere with the POC method. DOC concentration was measured in single water samples with a Dohrman carbon analyser (Baker and Eisenreich 1989).

Sediment samples were collected with a stainless steel box core (15 × 15 cm). The mechanical arm of the submersible was used to carefully push the corer into the sediment and rotate the trip mechanism which closed sliding doors under the sample. Three box cores were taken at two sites in the North Basin of Lake Michigan, two cores in Whitefish Bay, and a single core in the Caribou Basin of Lake Superior. After returning to the ship, each box core was subsampled with two 5-cm acrylic core tubes which were then refrigerated for less than 8 h before sectioning. Each subcore was extruded, and samples taken at 0–1 and 10–11 cm were placed in sterile Whirlpak bags. Samples were immediately removed from each section for bacterial counts. The material remaining from each section was frozen. After returning to the laboratory, each section was thawed and a sample (0.6–0.7 g wet) was weighed and then dried (100°C, 24 h) to determine the dry to wet ratio at both depths in all cores. Before the analysis of POC, the remaining material from each section was dried (100°C, 24 h) and ground with a mortar and pestle.

Bacteriological Methods

Water samples (10 mL) and sediment samples (0.5 g wet + 19 mL of distilled water) were preserved with formaldehyde (0.2-μm filtered; 2% final concentration) for counting bacteria, dividing cells, and all particles that were not recognizably bacteria or eukaryotic cells (diameter range 0.2–2.5 μm). All samples were refrigerated and counted within 2 wk after returning from the cruise. The number of bacterial cells was determined by epifluorescent direct counts (Zeiss microscope, total magnification 1250×) of DAPI-stained cells (Hobbie et al. 1977; Porter and Feig 1980). The relationship between temperature and bacterial abundance at each site was tested using linear regression of transformed data (e.g. cell density = a log (temperature) + b). Untransformed data were used to test the relationship between POC concentration and bacterial abundance.

Photographs of representative fields were made to determine cell and particle diameters. Bacterial dimensions were measured on projected photomicrographs with a graduated caliper and corrected for enlargement using a photograph of a stage micrometer. Cocci volumes were calculated assuming a spherical shape and rod-shaped cell volumes were estimated using the equation for a cylinder. Cell measurements from each sample were pooled prior to comparing sites.

The increase in bacterial abundance in the bottom water (BNL) after resuspending the SBL was predicted by adding the BNL bacterial density before resuspending the SBL and an estimate of the bacteria resuspended with the SBL. This estimate was made by measuring the increase in suspended solids in the BNL after resuspending the SBL and assuming that the bacterial density associated with this additional suspended material was the same as the surface sediment (0–1 cm depth). These predictions were compared with bacterial densities measured in the BNL after resuspending the SBL.

Synthetically active bacteria were counted in surface water and BNL samples to estimate the proportion of bacterial populations capable of growth (Kogure et al. 1980; Tabor and Neihof 1984). Nalidixic acid (0.025% wt/vol) and yeast extract (0.002% wt/vol) were added to 10-mL water samples incubated at the in situ temperature. After 6 h of incubation, samples were preserved with formaldehyde and refrigerated. Enlarged cells (≥2 times average cell diameter) in samples and controls killed with formaldehyde were counted by the epifluorescent technique and considered to be synthetically active.

Dividing bacterial cells at each site were counted to estimate the activity of bacterial communities in the water column (Hagström et al. 1979; Newell and Christian 1981). The influence of temperature on the FDC was tested at each site using a linear regression on transformed data (FDC = a log (temperature) + b). The FDC relationship to DOC concentration was examined by linear regression.

A growth experiment was carried out using water from the Caribou Basin to determine the relationship between the FDC and μ, the specific growth rate of bacteria (Newell and Christian 1981). Two water depths were examined; near the lake surface at 5 m and at 310 m, 1 m above the sediment. Water from each depth (900 mL) was filtered (0.2 μm) to remove bacteria and added to 100 mL of 0.8-μm filtered ("predator-free") water in sterile flasks. Two flasks of water from each

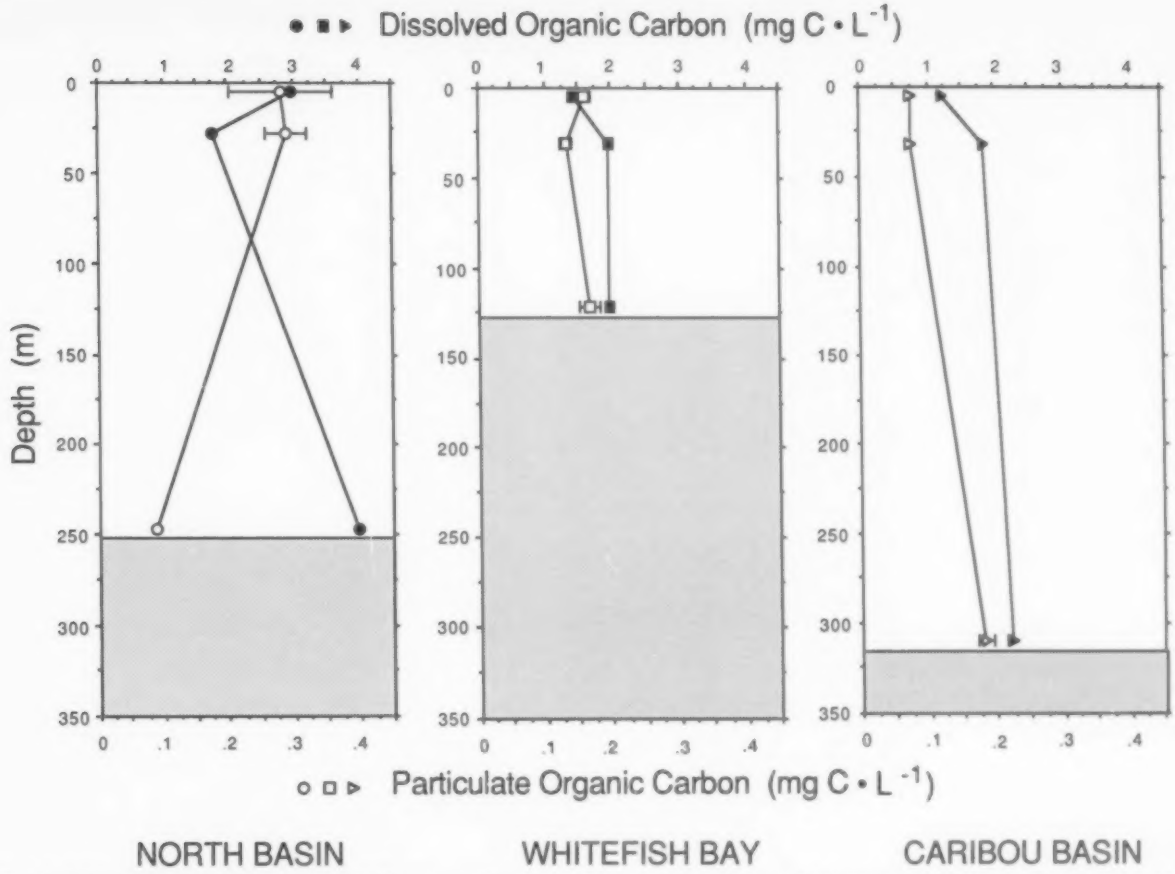

FIG. 4. DOC (solid symbols; $n = 1$) and POC (open symbols; $n = 2$) concentrations in Lake Michigan and Lake Superior during July 1988. Note that the scale for DOC concentration is 10 times greater than for POC concentration. Bars represent 1 SE of the mean for duplicate POC measurements.

depth had different concentrations of yeast extract added (25 and 50 mg·L^{-1}; DIFCO). A third flask was not enriched with yeast extract (0 mg·L^{-1}). The growth of bacterial cells in each flask was measured using direct counts of total cells and dividing cells. The specific growth rates (μ) between successive samplings were calculated for all flasks during the exponential phase of growth, yielding four estimates of μ for each water depth (Newell and Christian 1981). Only data from the flasks containing 0 or 25 mg yeast extract·L^{-1} were used in a linear regression to establish the relationship between μ and FDC because clear growth curves were not obtained in flasks with the highest yeast extract concentration (Newell and Christian 1981). We calculated the production of bacterioplankton in both the surface and bottom water of the Caribou Basin by estimating μ from the field FDC measurement and measuring the abundance and average cell volume of the bacterioplankton. These estimates of biovolume production were converted to carbon production using a conversion factor of 106 fg C·μm^{-3} (Nagata 1986).

Results

The three basins we visited exhibited different thermal and turbidity profiles (Fig. 1 and 2). A stratified water column and turbid hypolimnion were present in the North Basin of Lake Michigan. A stratified water column with a BNL in the hypolimnion was present in Whitefish Bay, Lake Superior. A thermally unstratified water column exhibiting no change in water transparency was observed in the Caribou Basin of Lake Superior. These water transparency patterns were corroborated by measuring particle densities by microscopy. There were more small particles in the deep hypolimnion (BNL) than at 5 m in the North Basin and Whitefish Bay sites (both p's < 0.05) but not in the Caribou Basin (Fig. 3; $p > 0.05$). A well-defined BNL was present in Whitefish Bay. Water transparency decreased rapidly below the thermocline and particle concentrations increased 10 times within 30 m of the sediment at this site. POC concentration appeared to decrease in the hypolimnion of the North Basin, Lake Michigan, and increase slightly at the Lake Superior sites, but these changes were not significant (Fig. 4; all p's > 0.05). DOC concentrations were higher near the sediment surface than in the epilimnion at all sites (Fig. 4).

Bacterial density was greater ($p < 0.01$) in the surface water and BNL of Lake Michigan compared with the Lake Superior sites (Fig. 5). The abundance of heterotrophic cells decreased from 4.7×10^6 cells·mL^{-1} at 5 m to 1.8×10^6 cells·mL^{-1} just above the sediment in the North Basin of Lake Michigan

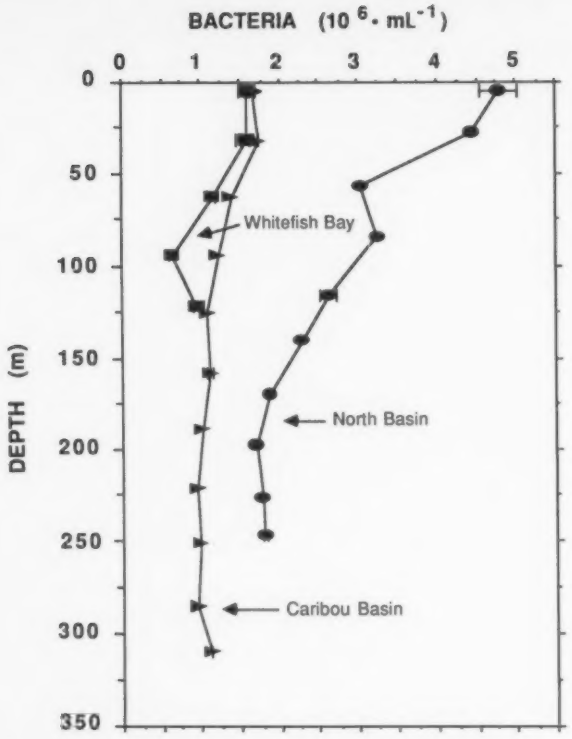

FIG. 5. Bacterioplankton cell density in Lake Michigan (North Basin) and Lake Superior estimated by direct counts of DAPI-stained cells. Bars denote the standard error of the mean when independent water samples were taken ($n = 3$).

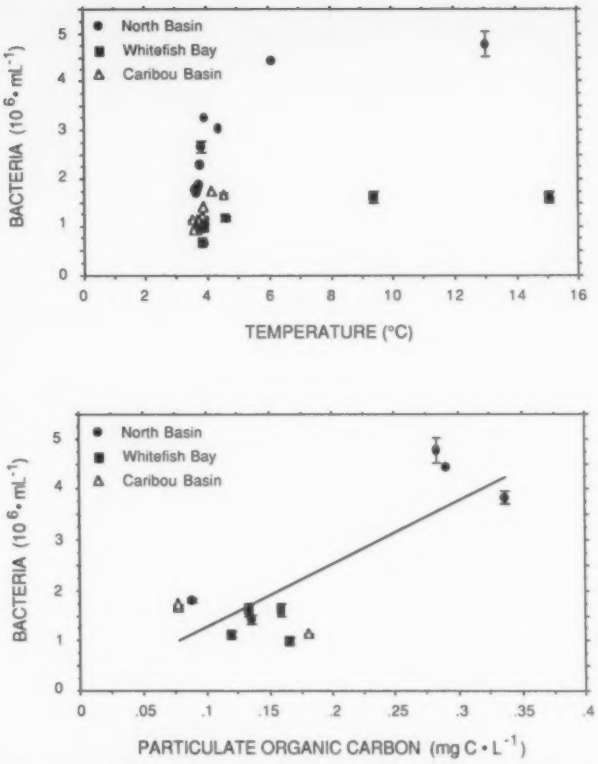
North Basin
Whitefish Bay
Caribou Basin
BACTERIA (10 6 · mL-1)
TEMPERATURE (°C)
0 2 4 6 8 10 12 14 16
North Basin
Whitefish Bay
Caribou Basin
BACTERIA (10 6 · mL-1)
0 .05 .1 .15 .2 .25 .3 .35 .4
PARTICULATE ORGANIC CARBON (mg C · L-1)

FIG. 6. Relationship between bacterioplankton density and water temperature (upper graph) and POC concentration (lower graph) in Lake Michigan (North Basin) and Lake Superior. Bars represent 1 SE of the mean for measurements from independent water samples ($n = 3$).

($p < 0.01$). Cell abundance was similar ($p > 0.05$) at 5 m in Lake Superior (1.6×10^6 cells·mL^{-1}) but decreased to slightly different ($p < 0.05$) densities 1 m above the sediment in Whitefish Bay (1.0×10^6 cells·mL^{-1}) and the Caribou Basin (1.1×10^6 cells·mL^{-1}). Bacterioplankton density increased with temperature at each site (regression r's > 0.86, all p's < 0.01), but this was more pronounced in Lake Michigan. Cell densities were higher in warmer water until a critical temperature (5–6°C) was reached in the North Basin, Lake Michigan, and Whitefish Bay (Fig. 6). Considering all sites together, high bacterial densities were observed in high-POC environments (Fig. 6; regression $r = 0.81$, $p < 0.01$).

Bacterial abundances in Lake Michigan surface sediment (4.7×10^9 cells·dry g^{-1}) and deep sediment samples (3.3×10^9 cells·dry g^{-1}) were slightly greater than Lake Superior sediments (1.9×10^9 and 0.7×10^9 cells·dry g^{-1}, respectively), but these differences were not significant ($0.05 < p$'s < 0.1). Similarly, the numbers of bacteria in surface sediment (0–1 cm) and deep sediment (10–11 cm) were not significantly different at each site ($p > 0.1$). The organic carbon concentration was similar ($p > 0.05$) in the surface sediment of Lake Michigan (4.0%) and Lake Superior (3.1%). There was more organic carbon in the deep sediment of Lake Michigan (3.2%) compared with Lake Superior (1.3%). The abundance of sediment bacteria was higher in sediments with a greater organic carbon concentration (regression $r = 0.81$, $p < 0.05$).

Cell density 1 m above the sediment was slightly smaller than the density in the midwater column ($p < 0.05$) but 1.5 times greater ($p < 0.05$) than the density 30 m above the sediment interface in Whitefish Bay (Fig. 5). Bacterial density did not increase from the midwater column to the deep hypolimnion (1 m above sediment) at the other sites ($p > 0.05$). Resuspending sediment from the SBL increased the density of bacteria in the BNL from 1 to 16%, depending on the site. These observed increases in cell density were similar to the changes predicted from the increased amount of particulate matter suspended in the BNL and the density of bacteria in the surface sediments (Table 1).

More than 99% of the cells observed at all sites were coccoid shaped. Cell volumes ranged from 0.024 to 0.042 μm^3 in water samples and from 0.032 to 0.046 μm^3 in sediments (Table 2).

TABLE 1. Changes in the density of bacteria in the bottom waters (1 m above sediment) of Lake Michigan and Lake Superior after resuspending surface sediment with the robotic arm of the *JSL-II* submersible. Predicted values were calculated from suspended solids before and after deliberately agitating the sediment.

Lake, basin	Dive number	Predicted change (%)[a]	Observed change (%)
Michigan, North Basin	1596	—	8.7
Michigan, North Basin	1599	1.3	1.1
Superior, Whitefish Bay	1604	7.8	15.9
Superior, Caribou Basin	1611	4.8	6.4

[a]Predicted = {[(sediment cells·g^{-1}) × (g·mL^{-1} "after" resuspension − g·mL^{-1} "before" resuspension)]/(BNL cells·mL^{-1} "before" resuspension)} × 100.

TABLE 2. Cell volume (μm^3) of bacteria in surface wter (5 m), bottom water (1 m above sediment), "fluff" (bottom water with resuspended sediment), and surface sediment (0–1 cm) in Lake Michigan and Lake Superior. From 5 to 113 cells were measured in samples from each lake. The mean and standard error of cell volumes measured in all samples are given.

Lake, basin	Surface water	Bottom water	"Fluff"	Sediment
Michigan, North Basin	0.031	0.027	0.034	0.046
	(0.002)	(0.002)	(0.003)	(0.013)
Superior, Whitefish Bay	0.028	0.042	0.028	0.032
	(0.011)	(0.014)	(0.003)	(0.002)
Superior, Caribou Basin	0.026	0.024	0.031	0.039
	(0.001)	(0.001)	(0.002)	(0.002)

TABLE 3. Percentage (± SE) of SAB cells in Lake Michigan and Lake Superior. Nalidixic acid was used to prevent cell division. Cells that enlarged (≥2 times average size) after 6 h were counted as synthetically active. A killed control was subtracted from three independent samples ($n = 3$). "Fluff" represents bottom water with resuspended surface sediment generated by the *JSL-II* submersible. There was no significant difference between sites or depths (all p's > 0.05).

Lake, basin	Dive number	Surface water	Bottom water	"Fluff"
Michigan, North Basin	1596	2.9	3.2	3.1
		(0.7)	(0.3)	(0.9)
Michigan, North Basin	1599	2.7	3.0	2.7
		(0.7)	(0.7)	(0.6)
Superior, Whitefish Bay	1604	2.4	2.6	4.6
		(1.4)	(0.6)	(1.3)
Superior, Caribou Basin	1611	3.4	2.0	2.4
		(0.4)	(0.3)	(1.3)

The cell volumes of bacteria in both lakes were similar in the water and in the surface sediment (all p's > 0.05). There was no significant cell volume difference between the bacteria in the water and surface sediment in the North Basin or Whitefish Bay (both p's > 0.05). In the Caribou Basin, where no turbid layer was observed, cell volumes in the surface water (5 m) and the bottom water (310 m) were smaller than cell volumes observed in the surface sediment ($p < 0.05$). This difference did not change after the SBL was resuspended ($p < 0.05$).

The number of SAB was less than 5% of the total number of bacteria in the epilimnion and hypolimnion within both lakes (Table 3). The numbers of SAB were similar in the surface and bottom waters at all of the sites we studied (all p's > 0.05). After the SBL was resuspended, the number of SAB in the bottom water did not change significantly at each site (all p's > 0.05).

The number of cells visibly dividing decreased with depth in both Lake Michigan and Lake Superior (Fig. 7). A similar percentage (4.6%) of the total number of cells were dividing 5 m below the surface of Whitefish Bay and the Caribou Basin ($p > 0.05$); this decreased to <2% near the sediment ($p < 0.05$). A smaller percentage of cells (≈3%) were dividing 5 m below the surface in the North Basin of Lake Michigan ($p < 0.05$). The FDC increased with temperature at all sites (regression r's > 0.86, all p's < 0.05). The FDC was higher in warmer water until a critical temperature (about 5°C) was reached in the North Basin and Whitefish Bay (Fig. 8). Considering all sites together, FDC was inversely related to DOC concentration (Fig. 8; $r = 0.70$, $p < 0.05$). This inverse relationship was significant ($p <$

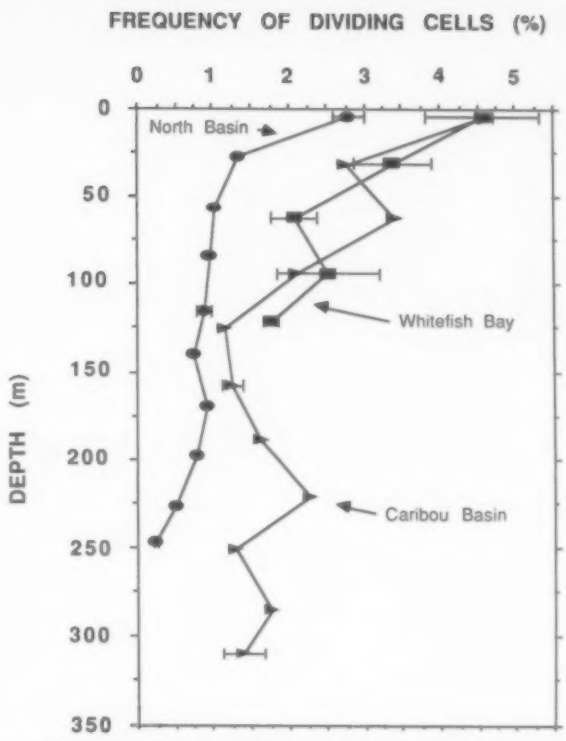

FIG. 7. Depth profiles of the FDC in Lake Michigan and Lake Superior during July 1988. Bars represent 1 SE of the mean for depths where independent water samples were taken ($n = 3$).

0.05) only in the Caribou Basin when individual sites were examined.

Significant relationships were observed between μ and FDC for bacteria from 5 and 1 m above the sediment in the Caribou Basin (Table 4). These regressions were used to estimate bacterial μ in the surface water and BNL of the Caribou Basin using field measurements of FDC. These growth rates correspond to doubling times ($0.693 \cdot \mu^{-1}$) of 29 h in the surface water and 231 h near the sediment–water interface (Table 4).

Discussion

The BNL started at the top of the hypolimnion in the North Basin, Lake Michigan. A well-defined BNL was observed near the sediment in the hypolimnion of Whitefish Bay. Upwelling may explain the absence of thermal and particle stratification at the Caribou Basin site (Fig. 2 and 3). Large-scale upwellings are common in Lake Superior and Lake Michigan (Mortimer and Csanady 1975; Lam 1978). A midlake upwelling zone in the Caribou Basin of Lake Superior has been predicted by water circulation simulations and has been observed (International Joint Commission 1976; Lam 1978).

Bacterial abundances in the bottom water of Lake Michigan have been observed to be about one half those in the surface water during the summer (Scavia and Laird 1987). We saw a similar decrease with depth; however, our measurement of abundance in the surface water of the North Basin was about 2.5 times those reported previously for Lake Michigan (Moll and Brahce 1986; Scavia and Laird 1987). This may have occurred because we used DAPI staining whereas acridine

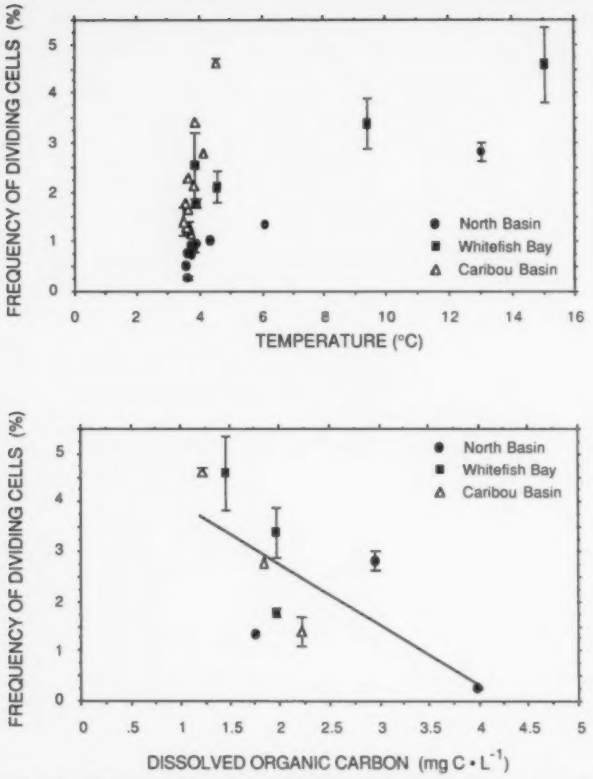

FIG. 8. Influence of temperature (upper graph) and DOC concentration (lower graph) on the FDC in Lake Michigan (North Basin) and Lake Superior. Bars represent 1 SE ($n = 3$).

orange was used in the other studies. DAPI counts are often higher than acridine orange direct counts, although this depends on the habitat (Porter and Feig 1980; Newell et al. 1986). Our measurements in Lake Superior were similar to other Great Lakes studies (Moll and Brahce 1986; Scavia and Laird 1987).

Bacterioplankton abundance was related to environmental temperatures in both lakes (Fig. 6), as it often is in marine systems (Tabor and Neihof 1984). The abundance of culturable, heterotrophic bacteria in the surface waters of Lake Superior is strongly correlated ($r = 0.90$) with temperature (Rao 1978). Moll and Brahce (1986) observed a weaker correlation ($r = 0.30$–0.42) between bacterioplankton abundance and temperature, but this relationship was stronger than correlations between bacterial density and nutrients. The bacterial cell volumes we measured in both lakes were within the range reported for bacteria in Lake Michigan (Scavia and Laird 1987).

Short-term resuspension of sediments does not cause a large increase in bacterioplankton density in the bottom waters of Lake Michigan or Lake Superior (Table 1). Similarly, the presence of BNLs did not affect the bacterioplankton abundances we observed in the hypolimnia of these lakes. Only in Whitefish Bay, where particle concentrations increased and transparency decreased quickly near the sediment, did we observe a significant increase in cell abundance (Fig. 2–5). The concentration of small particles increased 10 times in the BNL compared with the hypolimnion at this site, yet bacterial abundance increased only 1.5 times near the sediment.

TABLE 4. Specific growth rates (μ) for bacterioplankton in surface (5 m) and bottom water (310 m; 1 m above sediment) from the Caribou Basin, Lake Superior, estimated from the FDC.

Depth	Bacterial cells ($10^6 \cdot mL^{-1}$)	FDC (%)	μ (h^{-1})	Doubling time (h)
Surface water (5 m)	1.676	4.6	0.024[a]	29
Bottom water (310 m)	1.144	1.4	0.003[b]	231

[a]Surface water: $\ln \mu = 0.220\ FDC - 4.744$ ($n = 4$, $r = 0.91$, $F = 9.1$, $p = 0.09$).

[b]Bottom water $\ln \mu = 0.505\ FDC - 6.539$ ($n = 4$, $r = 0.97$, $F = 36.7$, $p = 0.03$).

Only 2.0–3.4% of the heterotrophic bacterioplankton in Lake Michigan and Lake Superior appear to be synthetically active during the summer, regardless of depth. Maki and Remsen (1980) observed higher concentrations of synthetically active bacteria in Lake Michigan (0.1–9.3% of total cells) than we did (Table 3). We subtracted killed controls from our values, however, to correct for the possibility of encountering unusually large bacterial cells, especially in BNL communities. The results of our work also suggest that the SAB method may not be a sensitive indicator of cell activity in low-temperature environments (Newell et al. 1986). The SAB method requires that bacteria grow and increase enough in size within 6 h to be visually perceptible. At the low temperatures encountered in the hypolimnia of the Great Lakes, this time period may not be long enough to allow all SAB to increase significantly in size. Longer incubation times might increase the sensitivity of the method, but Gram-positive bacteria unaffected by nalidixic acid could proliferate (Newell et al. 1986).

Our work has also demonstrated that few of the heterotrophic bacterioplankton present in Lake Michigan and Lake Superior are actively dividing. The FDC decreased at sites with higher DOC concentrations (Fig. 8). This seems counterintuitive upon first inspection. DOC concentrations, however, were lowest in the warmer epilimnia and highest in the colder bottom waters near the sediment in these lakes. Labile DOC concentrations are also lower in the epilimnion compared with the hypolimnion (4.5 versus 13% of DOC) during the summer in Lake Michigan (G. Laird, GLERL/NOAA, 2205 Commonwealth Blvd., Ann Arbor, MI 48104, USA, pers. comm.). Our observations support suggestions that heterotrophic bacterial production may be limited by dissolved organic matter (DOM) in surface waters of the Great Lakes during summer (Scavia and Laird 1987; Scavia 1988; Gardner et al. 1989).

A smaller percentage of the bacterioplankton were dividing in colder water (Fig. 8). Scavia and Laird (1987) observed that the rate of thymidine incorporation by bacterioplankton decreases as temperature drops below 8°C in Lake Michigan. Similarly, Pomeroy and Deibel (1986) observed that heterotrophic bacterial growth and respiration can be limited by low temperatures during phytoplankton blooms in the northern Atlantic Ocean. Our measurements and these observations indicate that temperature, in addition to DOC concentration, controls bacterial productivity, particularly in the colder hypolimnia of the Great Lakes.

The FDC has been used to estimate bacterial production in aquatic environments (Hagström et al. 1979; Newell and Christian 1981). The precision and sensitivity of this method have been questioned (Newell et al. 1986) because of technical factors (e.g. abundance of dividing cells, discriminating truely

TABLE 5. Comparison of bacterioplankton abundance (total direct count, TDC), SAB, and FDC and production of bacterioplankton in the Great Lakes and marine environments.

Location	Total direct count ($10^6 \cdot mL^{-1}$)	SAB (% of TDC)	FDC (% of TDC)	Production (mg $C \cdot m^{-3} \cdot h^{-1}$)
Oceanic	0.2–4.0[a]	0.7–7.9[b]	0.7–8[b]	0.02–6.4[a,c]
Coastal marine	0.2–21[c]	1.5–77[d]	2.5–10[c]	0.03–7.4[c,e]
Great Lakes	0.5–6[f,g,h]	7.1–9.3[f]	—	0.07–2.3[h]
Caribou Basin (5 m)	1.7	3.4	4.6	0.11
Caribou Basin (310 m)	1.1	2.0	1.4	0.01

[a]Cole et al. (1988).
[b]Kogure et al. (1980).
[c]Newell and Christian (1981).
[d]Tabor and Neihof (1984).
[e]Fuhrman and Azam (1980).
[f]Maki and Remsen (1980).
[g]Moll and Brahce (1986).
[h]Scavia and Laird (1987).

dividing cells) and the assumptions of this method (e.g. continuous exponential growth, calibration experiments). Our goal was to compare two communities at different water depths and not necessarily provide precise estimates of bacterial productivity at each site. We estimated that it takes >230 h for the bacterioplankton community to replace itself in the deep hypolimnion compared with about 29 h in the surface water of the Caribou Basin, using field FDC measurements (Table 4). Scavia and Laird (1987) found that thymidine incorporation, another estimator of bacterial production, decreased with depth in Lake Michigan.

Our results suggest that bacteria in the epilimnion are about eight times more productive than hypolimnetic bacterioplankton in the Caribou Basin. This implies that bacterioplankton may have a larger influence on nutrient cycling in the epilimnion of Lake Superior. This may not be true considering the great depth of the hypolimnion in this lake and the resuspension of particles from the SBL. Particle settling rates in the Great Lakes are about 1 $m \cdot d^{-1}$ (Eadie et al. 1984). Thus, most particles produced in the epilimnion would reach the sediment in the Caribou Basin within a year. Free bacteria in the epilimnion would be exposed to these particles only for a short period.

Sedimentation rates in Lake Superior vary from 0.1 to 0.7 $mm \cdot yr^{-1}$ (Johnson 1980; Johnson et al. 1982). At these rates of sediment accumulation, it would take 7–50 yr to replace the SBL, considering its estimated depth (5 mm). We observed from the submersible that sculpin commonly burrowed in the sediment and frequently resuspended the SBL while moving across the sediment. Several centimetres of sediment may be resuspended in this way before being buried, considering that bioturbation often mixes sediments deeper than the SBL. Even if bacterial production and mineralization is eight times slower in bottom water than in surface water, the bacterial community in the deep hypolimnion of Lake Superior may have 7–50 times longer than bacterioplankton in the epilimnion to use organic matter in their environment.

The abundance, activity, and production of bacterioplankton in Lake Michigan and Lake Superior appear to be similar to oceanic populations of heterotrophic bacteria (Table 5) and are not affected by the presence of a benthic nepheloid layer. The low bacterial abundance and productivity in the deep hypolimnia of these lakes appear to be controlled by the cold temperature of this zone. We suggest that the large organic matter losses observed in BNLs of Lake Michigan and Lake Superior are not due to greater bacterial abundance or activity in this zone, but may occur because organic matter is exposed for a longer time to mineralization by heterotrophic bacteria here than in the epilimnia of these lakes.

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A Sigmoid Model to Predict Gastric Evacuation Rates of Smallmouth Bass (*Micropterus dolomieui*) Fed Juvenile Salmon

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Rogers, J. B., and C. C. Burley. 1991. A sigmoid model to predict gastric evacuation rates of smallmouth bass (*Micropterus dolomieui*) fed juvenile salmon. Can. J. Fish. Aquat. Sci. 48: 933–937.

Laboratory experiments were conducted to examine the effects of water temperature, predator size, prey size, and prey number on gastric evacuation of smallmouth bass (*Micropterus dolomieui*) fed juvenile salmon. The smallmouth bass were allowed to feed voluntarily after 24–48 h of starvation and stomachs were pumped at intervals of 1–4 h until 90% of the stomach contents were evacuated (E_{90}). Evacuation approximated an *S*-shaped curve over time, and a sigmoid model was developed to predict evacuation at varying water temperatures, total meal weights, predator sizes, and prey number. The rate of evacuation increased with increasing water temperature, meal weight, or predator size. The E_{90} increased with larger meal weights but decreased with increasing temperature or predator size. E_{90} ranged between 4 and 95 h, depending upon conditions. E_{90} was slower than those estimated previously for another predator of salmon, the stomachless northern squawfish (*Ptychocheilus oregonensis*).

On a étudié en laboratoire les effets de la température de l'eau, de la taille des prédateurs et des proies et du nombre de proies sur l'évacuation gastrique chez l'achigan à petite bouche (*Micropterus dolomieui*) nourri de saumons juvéniles. Après une période de jeûne de 24 à 48 h, les achigans pouvaient se nourrir à volonté; leur contenu stomacal était ensuite recueilli au moyen d'une pompe à des intervalles de 1 à 4 h jusqu'à ce qu'il soit évacué à 90 % (E_{90}). La courbe d'évacuation en fonction du temps était à peu près sigmoïde; on a alors élaboré un modèle sigmoïde de prévision de l'évacuation pour des températures de l'eau, des tailles de prédateurs, des quantités de proies et des poids de repas divers. Le taux d'évacuation variait en raison directe de la température de l'eau, du poids du repas et de la taille des prédateurs. Le facteur E_{90} variait en raison directe du poids des repas, mais en raison inverse de la température ou de la taille des prédateurs. Il variait entre 4 et 95 h, selon les conditions. Par ailleurs, les E_{90} obtenus ici étaient inférieurs à ceux obtenus antérieurement chez un autre prédateur du saumon, la sauvagesse du nord (*Ptychocheilus oregonensis*).

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Reliable estimates of the amount of juvenile salmon consumed by smallmouth bass (*Micropterus dolomieui*) have not been possible because information about the gastric evacuation rates of smallmouth bass under various conditions is not available. Several studies have indicated that smallmouth bass consume outmigrating salmon (Warner 1972; Pflug and Pauley 1983; Gray et al. 1984; Gray and Rondorf 1986). Pflug and Pauley (1983) found that during periods of peak outmigration, salmonids were the major prey of smallmouth bass in Lake Sammamish, Washington. Lane and Jackson (1969) tested the voidance time (the time it took to pass all food from the fish) of *Daphnia* and fish fry in small (0.3–1.3 g) smallmouth bass at 12°C, but these results may not be generally applicable, since gastric evacuation may be affected by predator size (Swenson and Smith 1973; Jobling et al. 1977), size and type of meal (reviewed by Fänge and Grove 1979), and water temperature (Molnar et al. 1967; reviewed by Durbin and Durbin 1980).

Evacuation rates of smallmouth bass can be used not only in consumption estimates, but also have value in the assessment of consumption in relation to that of other predators of salmonids, such as the stomachless northern squawfish (*Ptychocheilus oregonensis*). We attempted to use experimental design and data analysis methodology similar to that used previously for northern squawfish (Beyer et al. 1988). Water temperature, prey size, and predator size ranges were selected for both smallmouth bass and northern squawfish to include natural conditions of predation on salmon in the John Day Reservoir, Columbia River (USA).

The primary objective of our study was to determine the rates of evacuation of smallmouth bass fed juvenile salmon at various water temperatures, prey weights, predator weights, and prey numbers and to express the rates in a single, easily applied equation. The secondary objective was to compare smallmouth bass evacuation rates with those of northern squawfish, another predator of juvenile salmon.

Methods and Materials

Laboratory Experimentation

Experiments were designed to minimize the correlation between the variables examined. Predators and prey were divided into three size groups and each combination of predator and prey was tested at each of three water temperatures. The amount of prey evacuated was examined by sampling fish at

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intervals of 1–4 h for each combination of prey size, predator size, and water temperature until evacuation approximated 90% (E_{90}). Emphasis was placed on obtaining at least five single-meal samples at each interval tested, with multiple-meal samples being obtained only when the smallmouth bass voluntarily ate more than one prey.

Smallmouth bass were collected from the John Day Reservoir, Columbia River (USA), and John Day River, Oregon, as needed and taken to tanks at the National Fisheries Research Center, Columbia River Field Station, Star Route, Cook, WA 98605. One to three predators from each size group (<200, 200–300, and >300 mm fork length) were randomly selected and placed in each tank; the size groups were separated by screen dividers. The smallmouth bass were acclimated to one of three water temperatures (10, 15, or 20°C) and a 12 h light : 12 h dark photoperiod over a period of 2 wk. Before the tests, the fish were starved 24–48 h (a period based on preliminary trials) in order to ensure that stomachs were empty. The smallmouth bass were used more than once, but at least 7 d elapsed between tests. The juvenile salmon prey (chinook salmon (*Oncorhynchus tshawytscha*) or coho salmon (*O. kisutch*) depending on availability) were obtained from the Little White Salmon and Willard National Fish Hatcheries, Cook, WA. Before use in the experiments, the salmon were weighed (±0.001 g) and marked with color-coded threads sewn between the dorsal fin and backbone.

Experiments were conducted from May 1985 to August 1986. Up to three prey of similar size (0.26–0.38, 1.0–1.8, or 3.0–5.0 g) were made available to the bass during the first hour of artificial light. Checks were made at 0.5-h intervals thereafter, with time of ingestion recorded as the midpoint of the interval in which feeding occurred. As soon as at least one of the prey was eaten, the remaining prey were removed. After a predetermined time, the smallmouth bass were anesthetized with approximately 80 ppm tricaine methanesulfonate (MS-222) or with approximately 50 ppm benzocaine and weighed to the nearest gram. Each stomach was flushed with water at 1.9 $L \cdot min^{-1}$ into a holding bucket. Stomach pumping of the smallmouth bass was continued until all the eaten prey were recovered (evidenced by obtaining the color-coded threads) and about 30 s had elapsed without any food items being removed. The pump consisted of a modification of the stomach sampler developed by Seaburg (1957). A single 0.64-cm copper tube was soldered to a threaded garden hose attachment and attached to a trigger action spray nozzle; water was pumped from a reservoir tank with a 12-V pump. The water and food material were strained through a 333-μm sieve to obtain the samples. The samples were weighed (±0.001 g) after preservation in 10% formalin for at least 2 wk.

Data Analysis

We generally formulated models by using multiple regression with varying transformations of food weight evacuated (grams) as the dependent variable (E); the best subset of independent variables was selected for each model using the Cp criteria (Neter et al. 1983; SAS Institute Inc. 1985). Selection of the best subset was based on achieving a Cp value which was both low, indicating a reduced mean square error, and close to the number of variables in the selected subset, indicating a lack of bias (Neter et al. 1983). For most of the models (linear, square root, and exponential), the possible independent variables included time, meal weight (the sum of all prey weights eaten), water temperature, predator weight, and number of prey. For the log–log transformation, the possible independent variables or their natural logarithms were included. After the independent variables were selected for each model, we made comparisons between the models on the basis of mean square error of the residuals using untransformed values (MSE) and examination of the residuals (Neter et al. 1983).

A new model was also developed to approximate the *S*-shaped curve of evacuation over time. This model was a modification of the von Bertanlanffy growth sigmoid equation based on weight (Cullen 1983):

$$(1) \quad \mathrm{Wt} = W_\infty (1 - \exp(-a(t - t_0)))^v$$

where Wt = weight at time t, W_∞ = maximum weight, a and v = fitted coefficients, t = time, and t_0 = time at weight 0. Equation (1) was used as a basis because we hypothesized that a food bolus would reduce during digestion in a manner similar to the way a prey fish would grow. The von Bertanlanffy equation is also more adaptable than the logistic equation because it allows the inflection point to vary, and it is preferable to the Gompertz growth curve, used by Medved (1985), because it can be expressed in linear form.

The von Bertanlanffy equation adapted to represent evacuation over time was

$$(2) \quad \mathrm{PE} = (1 - \exp(-at))^v$$

where PE = proportion evacuated (grams evacuated at time t/initial meal weight), a and v = fitted coefficients, and t = time. Equation (2) expressed in linear form is

$$(3) \quad \ln(1 - \sqrt[v]{\mathrm{PE}}) = -a(t)$$

where PE = proportion evacuated, t = time, and a and v = fitted coefficients.

To determine how this relationship changed with the other independent variables tested, we estimated the coefficient a for each sample by solving equation (3) for a, using the time and PE for the sample. The exponent v was assumed to be equal to 3.0 as it is for isometric growth (weight = length^3; Cullen 1983). Multiple regression with the Cp criteria was then used to predict a, given meal weight, predator weight, water temperature, and prey number as the possible independent variables. The independent side of the equation was then substituted in place of a in equation (2). To further improve the fit and use E rather than PE as the dependent variable, we multiplied both sides of that equation by initial meal weight and iteratively fitted the intercept of the substituted equation and the exponent v using the SAS nonlinear multivariate secant method.

Negative values for PE and E were dealt with differently, depending upon the transformation required. Since the logarithmic and square root transformations could not be run on data where the evacuation data were less than zero, for the general multiple regression transformations the negative values were set to zero. For the logarithmic models, which cannot be run with zero values, we then added 0.01 g to all data points. In the newly developed model, in estimating a, zero and negative values for PE were set to 0.00001, but in the final nonlinear fitting the values were not altered.

Results

The sigmoid model using meal weight, temperature, and predator weight as independent variables best predicted evac-

TABLE 1. Sample sizes and means of meal weight (g) and predator weight (g), stratified by temperature (°C), prey size group (g), and prey number.

		Samll prey group 0.33 g (0.26–0.38 g)			Medium prey group 1.5 g (1.0–1.8 g)			Large prey group 3.7 g (3.0–5.0 g)		
Prey no.	Temp. (°C)	Sample size	Mean meal weight	Mean predator weight	Sample size	Mean meal weight	Mean predator weight	Sample size	Mean meal weight	Mean predator weight
1	10	31	0.34	186	51	1.46	244	63	3.74	266
	15	42	0.32	205	58	1.40	252	84	3.68	284
	20	38	0.32	195	41	1.59	283	61	3.70	177
2	10	6	0.65	116	7	2.95	396	13	7.35	240
	15	4	0.63	174	20	2.86	160	11	7.48	389
	20	12	0.63	170	5	2.99	104	10	7.43	187
3	10	1	1.09	233	4	4.32	407	0	—	—
	15	0	—	—	4	4.42	290	4	11.39	426
	20	7	0.93	124	1	5.31	199	2	11.23	124

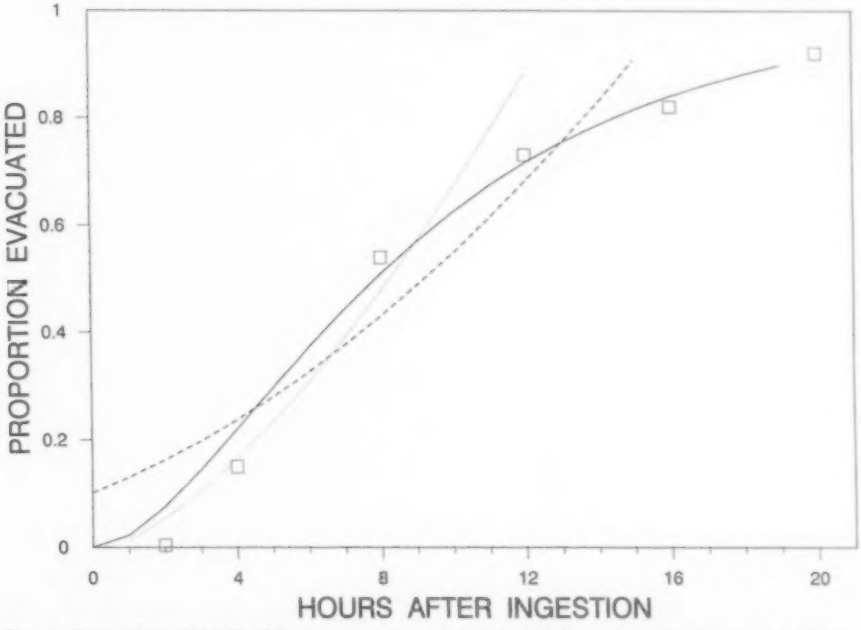

FIG. 1. Comparison of the fit of the squareroot (- - -) and logarithmic (···) transformations of the linear model versus the sigmoid model (——) for a 1.4-g meal, 15°C, 254-g predator. Symbols = means of 3–12 samples of medium meals (1.0–1.8 g) at 15°C.

uation of smallmouth bass fed juvenile salmon under the conditions tested. Prey number was not included in the model because its use increased both the Cp value and the bias, from a Cp of 3.6 for three variables to a Cp of 5.4 for all four variables. Correlations between the variables tested were generally low. The highest correlation was between meal weight and number of prey ($r = 0.40$), but this was reduced to 0.25 when the log transformation was applied to meal weight. The data set included 469 one-prey meals, 88 two-prey meals, and 23 three-prey meals, with prey weights ranging from 0.26 to 4.96 g and meal weights up to 12.01 g (Table 1).

The sigmoid model was better than the other models tested (Fig. 1), as shown by lower MSE values (Table 2) and residuals. The sigmoid model fitted to the evacuation data was

$$(4)\quad E = S(1 - e^{-0.005t\,S^{-0.29}e^{0.157T}W^{0.23}})^{1.95}$$

where E = grams evacuated, t = time (hours), S = meal weight (grams), T = water temperature (degrees Celsius), and W = predator weight (grams).

The sigmoid model indicated that the E_{90} increased with increasing prey weight, but decreased with increasing temperature and predator weight (Fig. 2). Predicted emptying times ranged from 4.5 h for one 0.26-g prey (0.04% body weight meal, eaten by a 650-g predator) at 20°C to 95 h for a 12.01-g meal (12.9% body weight, 93-g predator) at 10°C. E_{90} increased by about five times when the temperature was halved (Fig. 2A) and a little more than doubled when the predator weight decreased from 1550 to 29 g (Fig. 2B) or the prey weight increased from 0.26 to 5.0 g (Fig. 2C).

TABLE 2. Comparisons of equations expressing gastric evacuation in smallmouth bass (sample size 580). E = grams evacuated; t = time (h); S = meal weight (g); T = water temperature (°C); W = predator weight (g); N = number of prey; MSE = mean square error of the residuals.

Model	MSE	Fitted equations
Linear	0.35	$E = -2.49 + 0.10t + 0.26S + 0.12T + 0.001W$
Square root	0.33	$E = (-0.96 + 0.05t + 0.15S + 0.07T + 0.0003W)^2$
Exponential	4.17	$E + 0.01 = 0.0028\, e^{0.05t}\, e^{0.24S}\, e^{0.20T}\, e^{0.001W}$
Log–log	0.27	$E + 0.01 = 0.0003\, t^{1.49}\, S^{0.47}\, e^{0.20T}\, W^{0.24}\, e^{0.14N}$
Sigmoid	0.12	$E = S(1 - e^{-0.005t\, S^{-0.29}\, e^{0.15T}\, W^{0.23}})^{1.95}$

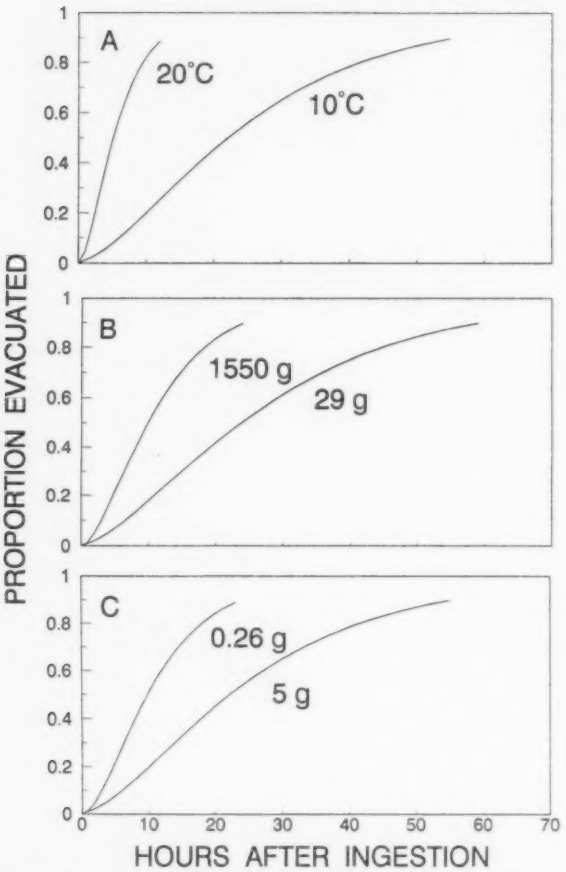

FIG. 2. Comparison of the effects of (A) increasing water temperature (with 5-g prey and 300-g predators), (B) predator weight (at 10°C and 1-g prey), and (C) prey weight (at 10°C and 300-g predators) on gastric evacuation in smallmouth bass.

The rate of evacuation (grams per hour) increased with increases in all three variables. The increase in E_{90} with prey weight was a result of an increase in the total weight evacuated; the amount evacuated per hour actually increased as the prey weight increased. For example, 90% evacuation of the 0.26-g prey was achieved in 22 h, but 90% evacuation of the 5.0-g prey took only 54 h (Fig. 2C).

Discussion

Our results imply that under the conditions tested, smallmouth bass consumption of salmon is potentially greatest when large smallmouth bass eat large meals in warm water. The faster a meal is evacuated from a predator, the more meals a predator is potentially capable of eating within a given time period. Incorporating our evacuation equation into a simple consumption model which assumes that predators eat meals which are 2% of their body weight and eat again when a meal is 90% evacuated, for example, a 600-g smallmouth bass could eat an average of 1.7 meals (20.4 g total) in a 24-h period at 20°C, but only 0.4 of a meal (4.8 g) at 10°C. Given the same assumptions, a 29-g smallmouth bass would averge at most three meals (1.8 g total).

Evacuation rates of smallmouth bass are slower than those of northern squawfish under comparable conditions, which suggests that northern squawfish are potentially more significant predators on salmon. Over the range tested (one prey of 4–5 g, predator of 170–1500 g, and water temperatures of 10–20°C), the smallmouth bass equation predicts 90% emptying times of 8–65 h whereas the northern squawfish equation (Beyer et al. 1988) predicts emptying times of 3–20 h.

Physiological explanations for our findings can only be hypothesized. The S-shaped curve of evacuation over time may be the result of several causes. The initial time lag could be caused if evacuation from the stomach begins only after a prey is broken down into pieces which are small enough to pass through the pyloric valve (Jobling 1986). The slowing of evacuation in the final stages could be caused by the decrease in the size of the food bolus, thereby lessening the peristaltic contractions and enzyme releases. The slowing could also reflect the slow passage of indigestible hard parts in the last 10% of evacuation (Karpevitch and Bakoff 1937), and some fish may have also been sampled after digestion was complete, but we attempted to lessen these effects by sampling only until evacuation approximated 90%.

At least a partial explanation of the difference in evacuation between smallmouth bass and northern squawfish may be that northern squawfish prefer lower water temperatures (16–22°C) (Brown and Moyle 1982) than do smallmouth bass, which prefer up to 27°C (Sigler and Sigler 1987; Ferguson 1958; McClane 1974) and show reduced feeding activity at or below 10°C (Scott and Crossman 1973). Northern squawfish evacuation was also nearly linear over time (Beyer et al. 1988), perhaps because the northern squawfish does not have a true stomach and initial lags caused by pyloric valve restriction of food movement would not occur.

Although it must be recognized that our equation is only an approximation of evacuation occurring naturally, we believe that biases from our methodology are minimal. It is possible that the two species of salmon used as prey in this study may evacuate at different rates, but this is unlikely given their similarity in body form, composition, etc. Our recovery of the remains of a meal using the lavage technique was apparently very effective, since we had little difficulty recovering the

threads which marked individual fish. This is in agreement with the findings of Seaburg (1957) and Brodeur (1984) who conducted postmortem examinations after flushing and estimated close to 100% recovery. Biases from our starvation period of 24–48 h would be expected to be slight, since Elliott (1972) found no effects on evacuation rates until fish were starved at least 6 d. There was no noticeable loss of appetite or abnormal behavior after the 7-d recovery period following anesthetizing.

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Chemosensory Attraction to Home Stream Water and Conspecifics by Native Brook Trout, *Salvelinus fontinalis*, from two Southern New England Streams

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Keefe, M., and H. E. Winn. 1991. Chemosensory attraction to home stream water and conspecifics by native brook trout, *Salvelinus fontinalis*, from two southern New England streams. Can. J. Fish. Aquat. Sci. 48: 938–944.

Behavioral preference tests were used to determine whether native brook trout, *Salvelinus fontinalis*, from two distinct populations could chemically discriminate home stream water and stock-specific cues. Juveniles and adults from a local anadromous population demonstrated significant preferences for home stream water and conspecifics when these stimulants were paired with groundwater. However, these trout did not prefer home stream water when paired with water from an unfamiliar stream, nor chemical traces of sympatric juveniles when paired with those of allopatric juveniles. Juvenile brook trout from a freshwater resident population displayed the same chemosensory responses as the anadromous trout, although they demonstrated distinct seasonal differences in their behaviors. These landlocked juveniles also preferred home stream water when paired with water from an unfamiliar stream. Anosmic trout maintained significant preferences for home stream water and water conditioned by conspecifics over control water, indicating that olfaction is not necessary for these attractions. Gustation may have a role in the behavioral preferences of trout.

Des tests de préférence comportementaux ont été utilisés pour déterminer si des ombles de fontaine indigènes, *Salvelinus fontinalis*, de deux populations pouvaient reconnaître chimiquement les eaux de leur cours d'eau d'origine et des signaux spécifiques au stock auquel ils appartiennent. Les juvéniles et les adultes d'une population anadrome locale ont montré une nette préférence pour les eaux de leur cours d'eau d'origine et leurs congénères quand ils étaient exposés à ces stimulus et à des eaux souterraines utilisées comme témoin. Cependant, ils n'ont pas reconnu leurs eaux d'origine auxquelles ils étaient exposés en même temps qu'à celles d'un cours d'eau non familier, ni les traces chimiques de juvéniles sympatriques auxquelles ils étaient exposés en même temps qu'à celles de juvéniles allopatriques. Les juvéniles d'une population d'omble d'eau douce ont montré les mêmes réponses chimiosensorielles que celles des ombles anadromes, mais leurs comportements variaient selon les saisons. Ces juvéniles confinés à l'eau douce ont de plus montré une préférence pour les eaux de leur cours d'eau d'origine par rapport à celles d'un cours d'eau non familier. Les ombles anosmiques continuaient de préférer leurs eaux d'origine et les eaux conditionnées par leurs congénères aux eaux utilisées comme témoin, ce qui montre que le sens olfactif n'est pas le seul à intervenir : la gustation pourrait jouer un rôle dans les préférences manifestées par les ombles.

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Adult anadromous salmonids return to their natal stream to spawn after a period of growth and feeding in estuarine or oceanic environments. Experimental evidence suggests that migrating adults identify their home stream by chemical cues which are present in the stream water (Hasler and Wisby 1951; Hasler and Scholz 1983; Brannon and Quinn 1990) or by population-specific pheromones released into the water by resident juveniles (Nordeng 1971, 1977). Although the source of the attractant(s) is still uncertain, it is generally accepted that salmonid juveniles imprint on a bouquet of odors specific to home stream waters (Harden Jones 1968), which they remember and utilize as returning adults. Chemical cues also may be used by juvenile salmonids to recognize population members (Stabell et al. 1982; Quinn and Hara 1985; Quinn and Tolson 1985), to establish, maintain, and identify a home range or territory (Stabell 1987), and to guide movements within a freshwater system (Stabell 1982).

Olfaction is most commonly cited as the chemosensory mechanism used by fishes in behaviours involving homing (Hasler and Scholz 1983; Stabell 1984) and recognition of population pheromones (Selset and Doving 1980; Quinn et al. 1983; Brannon et al. 1984; Stabell 1987). However, both olfactory and gustatory receptors are extremely sensitive in fishes and are capable of detecting certain amino acids and bile acids in minute concentrations (Doving et al. 1980; Hara et al. 1984; Groot et al. 1986; Rehnberg and Schreck 1986). Hara and coworkers have suggested that it is no longer prudent to assume that chemosensory behaviors are driven by olfaction and stressed the importance of investigating the role of gustation in fish behavior.

The purpose of this investigation was to determine if native brook trout, *Salvelinus fontinalis*, populations were attracted to home stream water and population-specific cues. In the Northeast region, brook trout exist as anadromous and freshwater resident populations. Anadromous brook trout have a well-developed homing ability (Whoriskey et al. 1981). Their olfactory rosettes are of comparable sensitivity to those of other sal-

monids (Hara et al. 1973; Thommesen 1983), yet there have been no behavioral tests designed to examine the use of olfaction by this species. We utilized individuals from both an anadromous and a freshwater population in an attempt to learn whether chemical recognition of home stream water and population pheromones varied with life history strategy. We expected that anadromous adults would exhibit a heightened discriminatory ability associated with their return migration. We also investigated whether a chemosensory mechanism other than olfaction was utilized in the behavioral discrimination of home stream and population cues by native brook trout.

Materials and Methods

Experimental Animals

Wild brook trout from a nonanadromous population in the Queen's River (Exeter, Rhode Island) and an anadromous population in Angeline Brook (Westport, Massachusetts) were used in these experiments. The Queen's River is a major watershed in southern Rhode Island. It has a substrate of primarily sand/silt, an abundance of aquatic plants, and a diverse fish fauna. Angeline Brook is a smaller, heavily shaded coastal stream. It is characterized by moss-covered rocks with intermittent areas of gravel, sand, or silt and only a few fish species. In addition to brook trout, these include the red fin pickerel, *Esox americanus*, and the American eel, *Anguilla rostrata*.

Between 30 and 40 young-of-the-year trout were electrofished from each stream during May and October of 1988. The fish were transported to the East Farm Aquaculture Facility at the University of Rhode Island where they were held in flow-through conditions under a simulated natural photoperiod. Young-of-the-year brook trout from the two populations were held in separate 250-L fiberglass bioassay tanks which were supplied with groundwater from a common source. The fish were acclimated to hatchery conditions for at least 3 wk prior to testing.

Sixteen adults were removed from the anadromous population in Angeline Brook during their migration upstream from the estuary in May of 1989. A fish trap, monitored daily from May 15 to June 1, was placed immediately upstream of the limit of saltwater intrusion in the brook. Captured fish were removed from the trap and transported immediately to the aquaculture facility (conditions same as juveniles). Attempts to acclimate and maintain nonanadromous adult fish for comparison with anadromous adults were unsuccessful.

Behavior Experiments

We conducted two sets of preference experiments with juvenile brook trout. The summer tests were executed from May 16 to August 1, 1988, and were followed by a winter series from November 16, 1988, to January 18, 1989. The preference experiments with Angeline Brook anadromous adults were carried out between July 4 and September 7, 1989. Individuals were initially tested for discrimination of home stream water and water conditioned by sympatric juveniles against control water (the groundwater source which was used to acclimate and maintain the trout for a minimum of 3 wk). If a significant preference was observed, the sample populations were tested for preference when home stream water was paired with water from an unfamiliar stream and when water conditioned by sympatric juveniles was paired with water conditioned by allopatric juveniles. To make certain that there was no bias in the experimental apparatus or any directional bias characteristic of the sample population, control tests were conducted pitting control water against control water, each season before any experimental trials took place.

An additional experiment was conducted using Angeline Brook juveniles in February of 1988. To determine if the behavioral preferences observed were mediated by olfaction, these trout were made anosmic by blocking the nares with a petroleum jelly plug (Rehnberg et al. 1985). Fish were anesthetized in 0.3% 2-phenoxyethanol. The petroleum jelly was heated to a slight boil (>150°C) and injected with a blunt needle and syringe into both anterior nares until it began to flow from the posterior nares. The petroleum jelly solidified immediately, blocking the olfactory passage. The trout resumed normal feeding activity within 24 h. Therefore, during the following week the anosmic trout were retested in choice tests where they had exhibited a significant preference. Finally, the trout were euthanized and each of the nares examined to ensure that the physical plug remained intact, functionally eliminating olfaction.

Stream waters were collected in 18.5-L containers on the same day that home stream preference experiments were conducted. Unfamiliar stream water was collected from Queen's River for tests involving Angeline Brook trout and from the Beaver River (West Kingston, Rhode Island) for tests with Queen's River trout. Using waterproof gloves, the containers were rinsed, filled until overflowing, sealed, transported immediately back to the aquaculture facility, and emptied into a randomly assigned source tank. As a precaution against losing a volatile component of the chemical signal in stream water, home stream preference experiments were conducted within 4 h of collecting stream waters. Juvenile conditioned source waters were produced by siphoning water from the 250-L tanks holding the juveniles from the respective populations. There were between 16 and 24 juveniles donors in each tank when generating conditioned waters. To make certain no food odors would contaminate the conditioned water, feeding was stopped, tanks were cleaned of debris, and tank water was flushed 24 h prior to siphoning. The conditioned water was siphoned from the tanks 30 min prior to the start of the preference tests.

The physicochemical nature of stream water is naturally different from the groundwater used as control water in these experiments. The groundwater used by the hatchery facility has a pH of approximately 7.0 and an alkalinity of 19.7 mg $CaCO_3$/L (Perrone and Meade 1977). During this study the pH of Angeline Brook water averaged 5.8 and the alkalinity averaged 1.9 mg $CaCO_3$/L. The pH of the water in the Queen's River averaged 5.9 and the alkalinity averaged 3.3 mg $CaCO_3$/L. The temperature of the source waters also differed depending on season. During the summer tests, temperature of stream waters and control water were determined to be within 1°C of each other. During the winter, however, the stream water was considerably colder than control water. Attempts were made to equalize the water temperatures by placing control water outdoors in 18.5-L carbouys while the stream waters were being collected. The temperature of stream water was within 2–4°C of that of control water during winter trials.

Tests with individual brook trout were conducted in two fiberglassed plywood troughs, 120 × 30 × 25 cm for juvenile experiments and 300 × 60 × 60 cm for adult tests (modified from Quinn et al. 1983; see Fig. 1). Eighty percent of the length of each trough was divided into two equal arms by a watertight

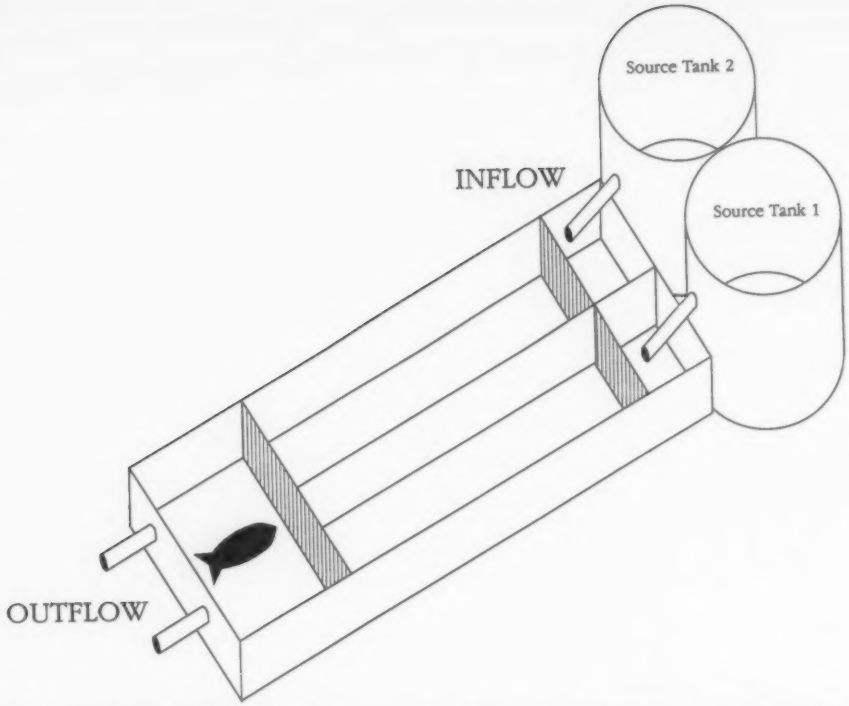

FIG. 1. Experimental apparatus for the preference tests. Dimensions of two-choice troughs used in juvenile experiments were 120 × 30 × 25 cm and for experiments with migratory adults were 300 × 60 × 60 cm. The fish figure is located in the holding area.

divider. The remaining length of each trough was partitioned by a gate and constituted a holding/acclimation area for the test fish.

During each test, trout were tested individually for preference between two water sources. Fish were placed in a darkened holding area and allowed to acclimate for 5 min. Dye trials indicated that 5 min was sufficient time for the stimulus waters to establish steady flows and infiltrate the holding area. Water was introduced from source tanks into the head of each arm of the trough by gravity. Flow commenced at the start of the acclimation period and continued throughout the test. Flow was calibrated to approximately 1 L/min in each arm of the trough at the beginning of each day's trials. At the end of the acclimation period, the screen covering the holding area and the gate were slowly lifted and the fish was allowed to swim freely for a 10-min test period. Water was completely drained and the preference troughs thoroughly rinsed between each trial. Source water was assigned randomly to each arm of the trough for each trial. All tests were conducted between 14:00 and 19:00 under dim red light.

During the test period the direction and time of each movement were recorded. The total time an individual trout spent in each arm was calculated. For each preference experiment, the response of the test population was analyzed using a Wilcoxon signed-rank matched-pairs test, which relies heavily on the consistency of responses within a test population. Significant preferences were determined at an alpha level of 0.05.

Only data from fish that sampled both water sources within the first half of the test period were included in the analysis. This prevented use of data from fish which did not move or moved little and did not clearly sample both water sources. Consequently, sample sizes varied from 12 to 25.

Results

Controls

Control fish always spent similar amounts of time in both arms of the preference trough (Fig. 2). The possibility of any directional bias can, therefore, be eliminated.

Juveniles

Young-of-the-year brook trout from the Angeline Brook population were attracted preferentially to both home stream water ($P < 0.01$) and water conditioned by sympatric juveniles ($P < 0.005$) over control water during both summer and winter (Fig. 2A). However, when home stream water was paired with unfamiliar stream water, Angeline Brook juveniles did not exhibit a significant preference ($P > 0.05$). They also did not demonstrate a significant attraction to water conditioned by sympatric juveniles when it was paired with water conditioned by allopatric juveniles ($P > 0.05$). The behavioral preferences observed for Angeline Brook juveniles were consistent between the summer and winter experiments.

Queen's River juveniles exhibited a more complicated, season-specific pattern of preferences (Fig. 2B). During the summer, these young-of-the-year trout preferred home stream water when it was paired with either control water ($P < 0.05$) or unfamiliar stream water ($P < 0.005$). However, no significant preference for home stream water ($P > 0.05$) was exhibited

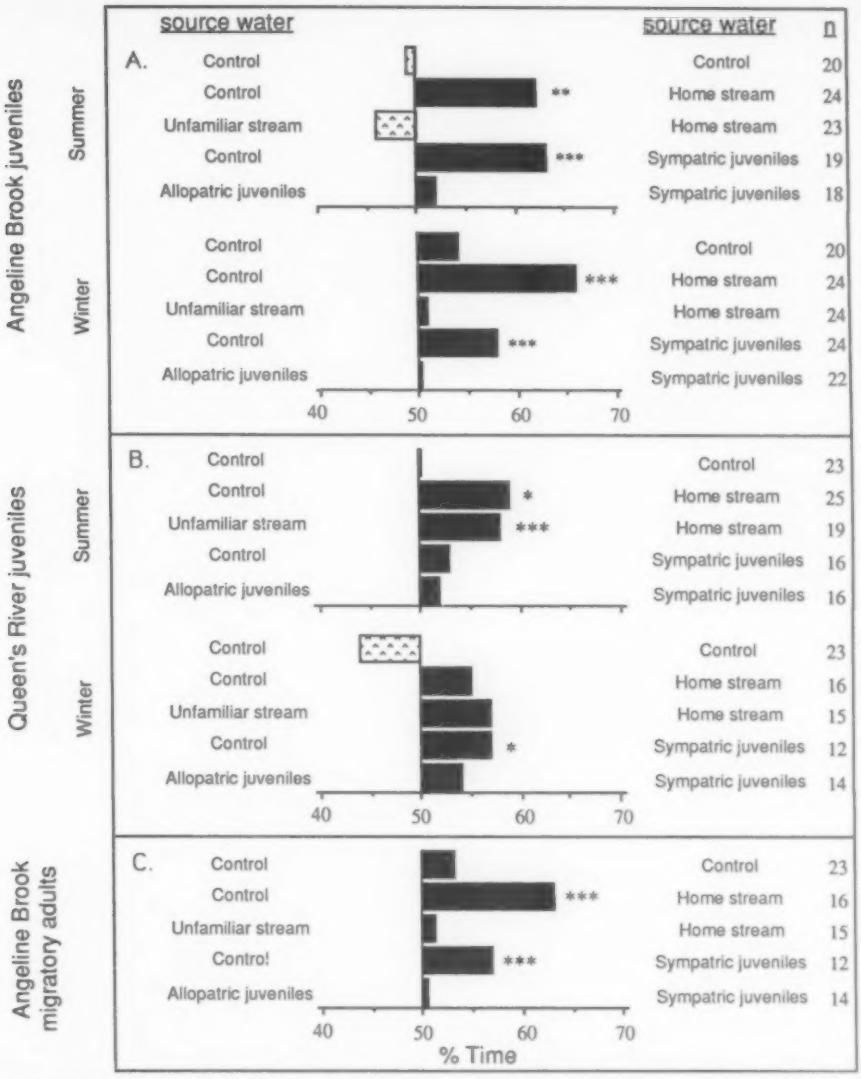

FIG. 2. Median percent time in different waters of brook trout in a two-choice preference trough. Percent time is the time an individual spent in the source water named on the right side of the figure divided by the total time the fish spent in both arms of the preference trough; 50% represents no preference. (A) Tests with juveniles from Angeline Brook during the summer of 1988 and the winter of 1988–89; (B) juveniles from the Queen's river during the same sampling period; (C) migratory adults from Angeline Brook during the summer of 1989. Numbers on the far right of the figure indicate sample size for each test. Asterisks denote significance of Wilcoxon signed-rank matched-pair tests (*$P < 0.05$; **$P < 0.01$; ***$P < 0.005$).

by Queen's River juveniles in either test during the winter experiments.

Queen's River juveniles preferred ($P < 0.05$) water conditioned by sympatric juveniles over control water in the winter. These were the only significant results obtained for the experiments testing population preference with Queen's River fish. Unlike the Angeline Brook juveniles, the Queen's River trout did not exhibit a significant preference for water conditioned by sympatric juveniles over control water ($P > 0.05$) during the summer.

Angeline Brook Migratory Adults

Migratory adults from Angeline Brook exhibited the same preference patterns as the juveniles (Fig. 2C). They showed a significant attraction to both home stream water ($P < 0.005$) and water conditioned by sympatric juveniles ($P < 0.01$) when paired with control water. These migratory trout did not demonstrate a significant preference for home stream water when it was paired with unfamiliar stream water ($P > 0.05$). They also did not show an attraction for chemical cues from sympatric juveniles over those from allopatric juveniles ($P > 0.05$).

TABLE 1. Median total time spent by normal and anosmic trout in different types of water when given a choice between two types at a time. Tests were conducted with juvenile brook trout from Angeline Brook during the winter of 1988–89. Experiment 1 tested home stream water (HSW) against control water (CW). Experiment 2 tested water from sympatric juveniles (SJ) against control water.

Experiment	Test group	Type of water	N	Median total time (min)	Wilcoxon signed-rank matched-pairs T	P
1	Normal	HSW vs. CW	24	270 138	−41	<0.005
	Anosmic	HSW vs. CW	23	288 149	−57	<0.010
2	Normal	SJ vs. CW	24	233 166	−55	<0.005
	Anosmic	SJ vs. CW	20	208 175	−42	<0.010

Anosmic Experiments

Anosmia was induced in 26 Angeline Brook juveniles in the winter of 1989. With their olfactory sense intact, these fish exhibited a preference for home stream water and sympatric juveniles over control water (Table 1). After being made anosmic, however, they were retested in trials pairing home stream water and sympatric juveniles with control water. Anosmic trout retained their preference ($P < 0.05$) for both home stream water and sympatric juveniles (Table 1). Examination of the nares of these juveniles revealed that the petroleum jelly plug was intact in all 52 snares.

Discussion

The attraction of native brook trout to home stream water corroborates research on coho salmon, *Oncorhynchus kisutch*, in which adults preferred home water over blank city water (Quinn et al. 1983; Brannon et al. 1984). The preference exhibited for sympatric juveniles is in agreement with several studies where other salmonids have demonstrated chemically mediated attraction to conspecifics (Doving et al. 1974; Olsen 1985; Groot et al. 1986; Stabell 1987). That brook trout populations show variation in their chemosensory behavior is also in accordance with previous investigations. Population differences in chemosensory behaviors, such as preference for home stream water or strain-specific attraction, are commonly observed (Quinn and Tolson 1985; Groot et al. 1986; Olsen 1986) and may reflect genetic heterogeneity as well as differences in sensory history due to local environmental conditions (Groot et al. 1986). It would not be prudent to attribute the population variability seen in this study to the anadromous and resident life history strategies adopted by these populations. Alternatively, the pattern of chemically mediated attraction in Queen's River juveniles may reflect population variation in behaviors such as territoriality and schooling.

Seasonal changes in chemoresponsiveness have been observed in Arctic char, *Salvelinus alpinus*, and Arctic grayling, *Thymallus arcticus* (Doving et al. 1980). The olfactory receptors of these fish became unresponsive to certain amino acids and bile acids in late August and did not regain responsiveness until the following spring. Similarly, Stabell (1987) found that juvenile Atlantic salmon, *Salmo salar*, recognized strain-specific cues in June, yet could not discriminate among strains when tested in November. Queen's River juveniles demonstrated a season-specific pattern of chemoresponsive behavior. They displayed attraction to home stream water during the summer, while attraction to conspecifics was the only response evident during the winter. The reason for seasonal changes in chemoreception, behavioral responsiveness, or stimulus production is unknown. Kleerekoper and Morgensen (1959) observed a similar decrease in behavioral responsiveness to olfactory stimuli in sea lamprey, *Petromyzon marinus*, which they suggested was the result of physiological changes associated with sexual maturation. Whether the changes observed for brook trout in this study correspond with seasonally changing physiological, behavioral, or ecological conditions remains to be investigated.

Several studies have found that migratory adult salmonids have heightened chemosensory ability and are able to recognize population- or strain-specific cues (Doving et al. 1974; Selset and Doving 1980; Quinn et al. 1983; Quinn and Tolson 1985; Groot et al. 1986). Furthermore, adult sockeye salmon, *Oncorhynchus nerka*, were attracted to home stream water when it was paired with water from several unfamiliar streams (Fagerlund et al. 1963). It is accepted that the heightened chemical attractions exhibited by migratory salmonids in the laboratory reflect homing to chemical cues by wild salmon. In this study, anadromous brook trout that were removed from the stream as they entered from the estuary did not demonstrate the same heightened chemical attractions of other salmonids that have been examined. These results suggest that anadromous brook trout from Angeline Brook do not utilize population pheromones or other chemical cues unique to their home stream during their return migrations from the estuary, although alternative explanations for this behavioral discrepancy may exhist. A lack of motivation is always a possibility when no preference is observed in behavioral tests. In addition, these adults may have been experiencing stress associated with captive conditions that influenced their chemosensory behavior. However, these trout fed actively and showed no signs of disease or any abnormal behavior commonly associated with chronic stress.

Reports on the migratory ability of anadromous brook trout are inconclusive. Anadromous brook trout are said to have a well-developed homing ability (Mullan 1958; O'Connor and Power 1973; Whoriskey et al. 1981). These studies, however, did not account for the 39–69% of the tagged brook trout that did not return to the home stream. White (1940, 1941) also found evidence for homing in brook trout in the Moser River, but it was complicated by a high incidence of error in choosing the appropriate home tributary.

Furthermore, the pattern of brook trout migration is not common among anadromous salmonids. Although there have been reports of brook trout migrating as much as 13 km through open ocean (Mullan 1958; Ritzi 1953; White 1942), sea-going trout more commonly remain in nearshore and estuarine waters (White 1940, 1942). Brook trout tend not to leave the influence of their home streams (Backus 1957; Power 1980; Whoriskey et al. 1981). As compared with other salmonids, the duration of their stay in salt water is shorter and more variable. Thus, homing mechanisms typical of other salmonids may not be uti-

lized in home stream migration of anadromous brook trout. After comparing the oceanographic features and migratory routes of sockeye salmon, Groot et al. (1986) concluded that chemical cues do not play a role in directing migrations in coastal waters. Hansen et al. (1987) showed that olfaction was inconsequential in the return migration of adult Atlantic salmon through coastal waters and into fresh water. Due to the coastal nature of anadromous brook trout migrations, a heightened discrimination of chemicals specific to their home stream may not be necessary. Since these trout remain within the influence of their home stream while in the estuary, a simple discrimination of presence versus absence of stream water, as demonstrated in this study, would be sufficient to guide their return.

Olfaction is the sensory modality commonly associated with many fish behaviors, particularly behaviors related to homing and pheromone recognition. The data from anosmic trout during this study indicate that the attractions to home stream water and sympatric juvenile chemical traces are maintained without olfaction. This finding does not eliminate a role for olfaction in brook trout chemical attraction. It does, however, demonstrate that other chemosensory receptors can mediate their behaviors. Our results are contrary to those of Hoglund and Astrand (1973) who found that juvenile Arctic char were no longer attracted to conspecifics after cauterization of the olfactory epithelium. However, their study was restricted by a very small sample size (only four trout were made anosmic) and large interindividual variation in response. The results of the present study are more in agreement with those of Hellstrom and Doving (1986), who showed that the bile acid taurocholate elicited feeding behaviors in both control and anosmic Atlantic cod, *Gadus morhua*. Thus, nonolfactory chemical senses can be important in mediating some behaviors of fish. It is important to emphasize here that the chemosensory responses demonstrated by anosmic trout in this study were very simple, requiring only the ability to discriminate presence versus absence of chemical cues.

Gustation is the most likely chemosensory modulator involved in the behavioral preferences exhibited by the anosmic brook trout. Research by Hara et al. (1984) demonstrated the high sensitivity of the gustatory system of rainbow trout, *Oncorhynchus mykiss* (formerly *Salmo gairdneri*), to bile acids. Bile acids are thought to be involved in the attraction of fish to other fishes (Selset and Doving 1980; Groot et al. 1986). Therefore, it is reasonable to suggest that gustatory detection of stimulants, such as bile acids, may have induced the preference for conspecifics by anosmic brook trout. Although the attractants involved in home stream preference are not known, stable bile acids are possible candidates (Doving et al. 1980). An alternative explanation exists for the attraction to home stream water exhibited by anosmic juveniles from Angeline Brook. Yamashita et al. (1989) showed that the gustatory system of rainbow trout is highly sensitive to the H^+ concentration of water. Furthermore, slight increases in H^+ concentrations have been shown to be attractive to Arctic char (Jones et al. 1985). In the present study, the pH of control water was maintained at approximately 7, while the pH of Angeline Brook averaged 5.8. Therefore, it is possible that the anosmic brook trout juveniles preferred stream water over control water due to brook trout bile acids contained in stream water and/or, perhaps, on the basis of the H^+ concentration.

In summary, native anadromous brook trout from southern New England demonstrated significant preferences for home stream water and conspecifics when paired with control water, but did not behaviorally discriminate between brook trout populations or between home stream water and unfamiliar stream water. These results suggest that anadromous brook trout may not rely on a bouquet of odors unique to their home stream waters to guide their migration from the estuary, although alternative explanations exist. Juveniles from the freshwater population displayed the same behaviors as the anadromous trout and also exhibited a home stream specific response. However, the preferences observed for the Queen's River juveniles changed between the summer and winter sample. Results of the anosmic experiments showed that a chemosensory mechanism other than olfaction was utilized in brook trout preference behavior.

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PERSPECTIVES

Genetic Effects of Cultured Fish on Natural Fish Populations

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Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural fish populations. Can. J. Fish. Aquat. Sci. 48: 945–957.

This paper addresses the genetic consequences of aquaculture on natural fish populations. The study is motivated by rapidly increasing numbers of intentionally and accidentally released fish and is based on empirical observations reported in the literature. A wide variety of outcomes, ranging from no detectable effect to complete introgression or displacement, has been observed following releases of cultured fish into natural settings. Where genetic effects on performance traits have been documented, they always appear to be negative in comparison with the unaffected native populations. These findings are consistent with theoretical considerations of the implications of elevated levels of gene flow between cultured and locally adapted natural populations; they raise concerns over the genetic future of many natural populations in the light of increasing numbers of released fish. Strategies for the genetic protection of native populations from the effects of aquaculture are outlined including more secure containment, the use of sterilized fish, and modifying the points of rearing and release. We recommend strong restrictions on gene flow from cultured to wild populations and effective monitoring of such gene flow.

Cet article porte sur les conséquences génétiques de la pisciculture sur les populations naturelles de poissons. L'étude de cette question est motivée par le fait qu'un nombre rapidement croissant de poissons d'élevage sont libérés intentionnellement ou accidentellement; elle est basée sur les observations empiriques relatées dans la documentation traitant du sujet. On a observé toutes sortes de conséquences à la suite de la libération de poissons d'élevage en milieu naturel, depuis l'absence de tout effect décelable jusqu'à l'introgression ou le remplacement complets. Dans les cas où l'on fait état d'effets génétiques sur les caractères de rendement, il semble que la comparaison soit toujours favorable aux populations non touchées. Ces constatations convergent avec les considérations théoriques émises quant aux effets d'un flux génétique important entre des populations d'élevage et des populations naturelles adaptées à leur milieu; elles portent à s'inquiéter pour l'avenir des caractères génétiques d'un grand nombre de populations naturelles étant donné le nombre croissant de poissons qui sont libérés. Il est question dans les grandes lignes des stratégies auxquelles on peut recourir pour assurer la protection génétique des populations indigènes contre les effets de la pisciculture : confinement plus sûr, utilisation de poissons stérilisés et changement des points d'élevage et de libération. Nous recommandons de restreindre fortement le flux génétique entre les populations d'élevage et les populations sauvages et de soumettre ce flux à une surveillance efficace.

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The recent acceleration of marine aquaculture in temperate waters throughout the world has raised questions about the genetic effects of these activities on natural populations (Maitland 1986). In particular, cultured salmonid fishes are being released in large numbers, both intentionally in the context of sea ranching and accidentally as escapees from closed culture operations. Cultured fish commonly represent genetically exogenous populations or crosses between them; in addition, the genetic constitution of culture populations has frequently been altered through inbreeding, selective breeding, or domestication (e.g. Allendorf and Ryman 1987; Gjedrem et al. 1988). Thus, cultured fish typically represent gene pools which are distinct from the natural populations with which they may come in contact. In many spawning populations, released fish now outnumber wild fish (Gausen and Moen 1991), an observation which brings an urgent focus to the need for conservation of natural populations.

In this paper we review the genetic effects that have occurred following releases of cultured fish into natural environments. We focus on salmonid fishes because information from this group provides — to our knowledge — the best available data

set for this task. First, salmonid fishes are well known genetically and ecologically. They are characterized by the existence of a number of local populations which exhibit a large degree of differentiation between them. The existence of striking morphological and ecological differences among conspecific local populations of salmonids has long been a well-established fact (e.g. Behnke 1972; Ricker 1972). More recently, numerous studies have shown that local salmonid populations typically are genetically distinct (e.g. Allendorf and Utter 1979; Ryman et al. 1979; Ryman and Utter 1987). This pattern of morphological and genetic differentiation seems to characterize all salmonid species, although considerable quantitative differences exist among species with respect to the amount of divergence (Ryman 1983). Second, it appears that much of the morphological and ecological divergence among local populations reflects local adaptation (e.g. Ricker 1972; Riddell et al. 1981; Taylor 1988). Third, salmonid fishes have been artificially reared and released for more than a century, and in considerable numbers including a variety of life stages (egg, fry, parr, smolt, and adult). Finally, many releases have been to environments inhabited by indigenous conspecific populations.

We are particularly concerned that the threats to genetic variation both within and among natural populations may not be recognized in time to protect the genetic integrity of local populations, and in some cases may even compromise the genetic population structure of the entire species. Our concerns reflect a general awareness of the need for genetic conservation of biological resources that has been well documented over the past 10 yr for fishes (Billingsley 1981; Ryman 1981a; Meffe 1987; Ryman and Utter 1987) as well as for Earth's living biota at large (Schonewald-Cox et al. 1983; Soulé 1986; Wilson 1988).

Our concern contrasts with the view of some workers who consider the genetic effects of large-scale releases with a more benign — and even positive — attitude. For example, Mathisen and Gudjónsson (1978) argued against a purist opposition to mixing gene pools of Atlantic salmon (*Salmo salar*) for release, stating that the similarity of environmental conditions encountered by those populations "eradicates the primary basis for evolution of widely different genotypes in individual streams." Kapuscinski and Lannan (1984) even suggested that natural populations may be genetically enhanced by increasing gene flow beyond natural levels from translocated natural or cultured stocks. Similarly, a mistaken attitude to the potential genetic effects of escaped fish on natural populations appears prevalent among some aquaculturists (cf. Sattaur 1989).

Throughout the paper we make no firm distinction between escapes from contained culture and intentional releases because both result in exogenous fish coming into contact with native populations. We present evidence indicating that (1) the genetic consequences of releases of cultured salmonids into the natural environment are frequently unpredictable and (2) interbreedings among exogenous and local salmonid populations are generally disadvantageous to the local ones. Consequently we make specific recommendations as guidelines for effectively dealing with the present concerns, including the responsibility of the culturer for monitoring the genetic effects of releases of cultured populations.

Intentional and Accidental Releases

Large numbers of cultured fish are intentionally released annually in contexts such as sea ranching and stocking for sport and commercial fisheries. For example, the numbers of salmonid smolts released for sea ranching purposes range from 8 million Atlantic salmon into North Atlantic and Baltic drainages to more than 4 billion Pacific salmon (chum (*Oncorhynchus keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), and chinook salmon (*O. tshawytscha*)) into North Pacific drainages (Isaksson 1988).

The intended fate of intentionally released fish is usually for most of them to be harvested at a marketable size upon returning to the point of release, with the gametes of the remainder being collected for cultured production of the subsequent generation. Although the magnitude of incidental natural spawning resulting from such releases does not appear to have been closely monitored, it does occur and has been repeatedly reported. For example, intentionally released fish have been documented to represent up to 80% of local spawning populations of coho salmon (Anonymous 1987b) and rainbow trout (*Oncorhynchus mykiss*, formerly *Salmo gairdneri*) (Chilcote et al. 1986).

Concerning accidental releases of cultured fish, most empirical data are from Atlantic salmon in Norway. The number of escaped Atlantic salmon from fish farms along the Norwegian coast has increased dramatically, roughly following the increase in aquacultural production, which has doubled every second year since 1970 and reached 115 000 tons in 1989. During the same period, the yield of wild Atlantic salmon was stable at 1200 tons in Norwegian home waters and at 300 tons in Norwegian rivers (Anonymous 1989a). Salmon accidentally escape from net pens that are wrecked during storms, or damaged by seals, otters, and daily wear and tear. For example, during storms in December 1988 and January 1989, an estimated 1.2 million salmon (more than 1200 tons) escaped from Norwegian fish farms; these accidental releases alone are equivalent to the total annual catch of wild Atlantic salmon in Norway.

Escaped Atlantic salmon (distinguished from wild fish on the basis of differences in fin and body morphology and scale characteristics; Lund et al. 1989) are finding their way to Norwegian rivers in increasing numbers. A survey of the proportion of farmed fish in rivers of southern Norway revealed that in 1987 and 1988, averages of 13 and 28%, respectively, of the spawners were escapees from net pens (Gausen 1988; Moen and Gausen 1989). In areas of intense fish culture, up to 80% of the spawners were of farmed origin (Fig. 1).

Examples of escaped salmonids entering rivers can also be found in other countries with net-pen culture. In a fish trap on the Burrishoole River, Ireland, 4% of the ascending Atlantic salmon in 1986 were of farmed origin (Anonymous 1987a), and that proportion increased to 28% in 1988 (Anonymous 1989b). In the River Lochy, Scotland, escaped Atlantic salmon formed almost 20% of the catches in 1988 (Anonymous 1990), and in Puget Sound, Washington, USA, escapees of Atlantic salmon from a growing pen culture have been observed both in fresh and salt water over a broad geographic range (O'Connor 1989; R. Giest, Washington Department of Fisheries, pers. comm.). Similarly, coho salmon, experimentally released from net pens in Puget Sound, produced an estimated annual number of 700–4000 spawners in local streams, where a total of 11 000 coho salmon are expected to spawn (Rensel et al. 1988).

Do released fish reproduce in the wild? A limited set of data answers this question in the affirmative for both intentionally and accidentally released fish. For example, sea-ranched Atlantic salmon (Jonsson et al. 1990) and hatchery-produced steelhead trout (anadromous rainbow trout; Chilcote et al. 1986;

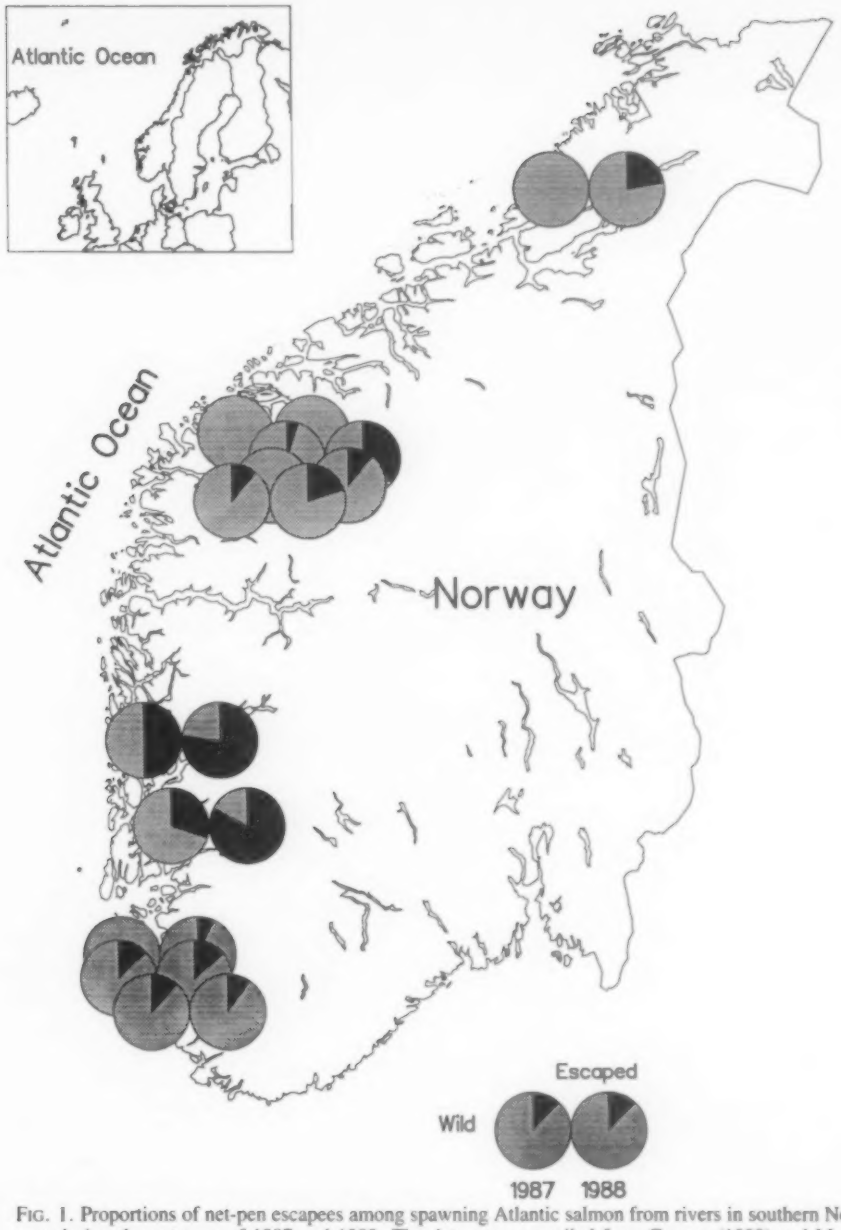

FIG. 1. Proportions of net-pen escapees among spawning Atlantic salmon from rivers in southern Norway during the autumns of 1987 and 1988. The data were compiled from Gausen (1988) and Moen and Gausen (1989), including only rivers where no Atlantic salmon smolts have been released. Total sample sizes are $N = 194$ and $N = 570$ for 1987 and 1988, respectively.

Leider et al. 1990; Campton et al. 1991) have been shown to reproduce successfully in nature. Similarly, spawning of pen-reared Atlantic salmon escaping to Norwegian rivers has been documented on the basis of observations of distinct pigmentation differences between the eggs of wild and pen-reared fish (Lura and Sægrov 1991a, 1991b). In two rivers having high proportions of escaped fish among the spawners, the proportion of redds containing eggs of pen-reared fish was 15 and 38%, respectively, clearly indicating the potential for successful reproduction. The reproduction of escaped females did not appear to be considerably different from that of wild fish. In the River Oselven where such an estimate could be made, 38% of the redds ($N = 8$) contained eggs from escaped females whereas the proportion of escaped fish among female spawners was 56% ($N = 52$; V. Moen, Norwegian Institute for Nature Research, Trondheim, pers. comm.).

Empirical Observations of Genetic Effects of Exogenous Fish on Local Populations

In this paper we report any finding that we consider relating directly or indirectly to past, current, or future genetic effects

TABLE 1. Observations bearing on the genetic effects that cultured salmonids may have on indigenous populations of the same or closely related species.

Trait studied	Species (region)	Observation	Reference
Genetic structure	Atlantic salmon (*Salmo salar*) (Norway)	Landlocked salmon not detectably affected by releases of offspring of anadromous salmon	Vuorinen and Berg 1989
	Atlantic salmon (Spain)	Some interbreeding between introduced hatchery stock of Scottish origin and local stocks	Garcia de Leániz et al. 1989
	Brown trout (*S. trutta*) (Sweden)	Local genetic structure broken down, presumably as a result of releases of hatchery stock	Ryman 1981b
	Brown trout (Northern Ireland)	Released hatchery stock reproduces successfully and interbreeds with local stocks	Taggart and Ferguson 1986
	Brown trout (France)	Introgression rates of 0–80% between released hatchery stock and local stocks	Guyomard 1989
	Brown trout (Spain)	Partial or complete displacement of genetically distinct native populations with genetically homogeneous hatchery fish	Garcia-Marin et al. 1991
	Chinook salmon (*Oncorhynchus tshawytscha*) (USA, Canada)	Genetic homogenization in areas of intense culture; heterozygosity and number of alleles the same in comparable wild and hatchery populations	Utter et al. 1989
	Chum salmon (*O. keta*) (Naiba R., USSR)	Gene frequencies of transplanted population displace those of indigenous stock	Altukhov 1981
	Rainbow trout (*O. mykiss*) (Kootenai R., Montana, USA)	Some native populations persist in spite of introduced stocks; admixture also seen	Allendorf et al. 1980
	Rainbow trout (Idaho, USA)	Local genetic structure not detectably affected by introduction of hatchery rainbow trout	Wishard et al. 1984
	Rainbow trout (Yakima R., Washington, USA)	Local genetic structure represents an admixture of introduced and native stocks	Campton and Johnston 1985
	Rainbow trout (Skagit R., Washington, USA)	Local genetic structure not detectably affected by introduction of hatchery stocks	D. Campton, (Pers. comm.)
	Rainbow trout (Washington, USA)	Little genetic differentiation among wild populations probably a result of releases of hatchery stocks	Reisenbichler and Phelps 1989
Hybridization	Atlantic salmon (Newfoundland, Canada)	Increased rate of hybridization between Atlantic salmon and brown trout in areas where brown trout have been introduced	Verspoor 1988
	Atlantic salmon (Spain)	High hybridization rates with brown trout where exogenous Atlantic salmon have been planted	Garcia de Leániz and Verspoor 1989
	Cutthroat trout (*O. clarki*) (western USA)	Extensive hybridization in areas where nonnative subspecies and rainbow trout have been introduced	Allendorf and Leary 1988
Stock size	Atlantic salmon (Norway)	Eradication of local stocks following introduction of fish from hatcheries infected by *Gyrodactylus salaris*	Johnsen and Jensen 1986
	Chum salmon (Naiba R., USSR)	Total stock size declines to 5% of original number after mass introduction of eggs from foreign stocks	Altukhov 1981
	Coho salmon (*O. kisutch*) (Oregon, USA)	Decline in juvenile densities in stocked streams despite high densities of wild plus stocked juveniles in the previous generation	Nickelson et al. 1986
	Coho salmon (Oregon, USA)	Sea ranching indirectly reduces natural production in apparent absence of displacement or introgression	Anonymous 1987b
Juvenile survival	Brown trout (New York, USA)	Survival of wild fingerlings higher than that of hatchery produced fingerlings	Schuck 1948
	Rainbow trout (Washington, USA)	Fry of wild origin have higher survival than either fry of hatchery origin or hybrid fry	Reisenbichler and McIntyre 1977
	Rainbow trout (Washington, USA)	Natural offspring of hatchery-produced fish survive less well than those of wild stock	Leider et al. 1990

TABLE 1. *(Concluded)*

Trait studied	Species region	Observation	Reference
Juvenile physical fitness	Brook trout (*Salvelinus fontinalis*) (New York, USA)	Stamina in offspring of wild parents higher than in offspring of domestic parents	Green 1964
Territorial behavior	Atlantic salmon (Sweden)	Weaker territorial behavior in offspring from hatchery stock than from wild stock	Norman 1987
Concealment behavior	Brook trout (New York, USA)	Offspring of domestic fish do not seek shelter and are less frightened by human presence than offspring of wild fish	Vincent 1960
Ocean survival	Atlantic salmon (Canada)	Hatchery-reared salmon have lowered survival when released in rivers other than their own	Ritter 1975
Ocean and river recapture rate	Atlantic salmon (Norway)	Hatchery stock from the nearest river similar to the local one; recapture rate of hatchery stock from distant river 50% lower	Hansen et al. 1989
	Coho salmon (Oregon and Washington, USA)	Negative relationship between recapture rate (relative to local stock) and distance transferred from natal stream	Reisenbichler 1988
	Masu salmon (*O. masou*) (Japan)	Recapture rate of transplanted stock about one tenth of that of local stock	Mayama et al. 1989
River recapture rate	Atlantic salmon (Spain)	Recapture rate of transplanted hatchery stock about one fifth or less of that of local stocks	Garcia de Leániz et al. 1989
Straying rate	Pink salmon (*O. gorbuscha*) (British Columbia, Canada)	Lower straying rate in offspring from local stock than in either foreign stock or hybrid offspring	Bams 1976
	Masu salmon (Japan)	No evidence of increased straying of transplanted stocks	Mayama et al. 1989
Return rate	Atlantic salmon (New Brunswick, Canada)	Lower return rates following crossbreeding of stocks	Bailey 1987
	Chinook salmon (Washington, USA)	Higher return rate of native stock than of either foreign stock or hybrid offspring	Brannon 1982
	Chum salmon (Sakhalin, USSR)	Inverse association between return rate of transplanted stock and its genetic distance from local stock	Altukhov and Salmenkova 1987
Prespawning survival	Masu salmon (Japan)	Lower survival between river entry and spawning for transplanted than local stock	Mayama et al. 1989
Disease resistance	Atlantic salmon (Norway)	Susceptibility to vibriosis much higher in one stock from the Baltic than in 14 stocks from Norway	Gjedrem and Aulstad 1974
	Atlantic salmon (Norway)	Susceptibility to *G. salaris* much higher in two Norwegian stocks than in one stock from the Baltic	Bakke et al. 1990
	Coho salmon (Oregon, USA)	Susceptibility to *Ceratomyxa shasta* higher for foreign stock than for either local stock or hybrid offspring	Hemmingsen et al. 1986

on recipient populations (Table 1). Our compilation of observations may be considered an extension of an earlier review by Ricker (1972) who reported the results of a large number of release experiments in various species of Pacific salmon. The present paper broadens the scope of that of Ricker by also including observations on purely genetic variation detected by molecular procedures developed subsequent to the studies that Ricker reviewed.

The impact of exogenous individuals on wild populations can be summarized in three general categories: interbreeding, competition, and contamination (i.e. introduction of pathogens). A direct genetic effect on recipient populations is obvious in the first category, but there may be a genetic basis for the effects of the other two categories as well. For example, competition from exogenous fish may weaken a native population through severe reductions in population size that may result in inbreeding and loss of genetic variability or, in the extreme case, to extinction of its gene pool. Likewise, a genetically resistant stock may carry pathogens and introduce them following translocation to an area where resistance has not developed. We have included these and similar observations as examples of actual or possible genetic effects caused by interactions between cultured and wild fish. To clarify the presentation, we have divided our examples into those that pertain to the genetic structure of

the wild populations (detected as differences of genotype and allele frequencies at loci that are identified by various molecular techniques) and those that refer to performance traits (that may have a heritable basis and represent local adaptation).

Genetic Structure

A wide variety of outcomes has been observed following natural reproduction of cultured fish (Table 1). At one extreme is displacement of indigenous stocks from massive introduction of exogenous fish. Such displacement appears to have been approached following mass transfer of chum salmon eggs from the Kalininka River to the Naiba River on Sakhalin Island, USSR, where gene frequencies of the donor population characterized parts of the run during the first generation after transfer (Altukhov 1981). In subsequent generations, no trace of the donor population was evident in the genetic data, but the total return to the Naiba River fell dramatically as compared with the undisturbed Kalininka River.

Introgression of native and exogenous cultured populations has been observed in many instances, e.g. in brown trout (*Salmo trutta*) of Northern Ireland and France (Taggart and Ferguson 1986; Guyomard 1989), in rainbow trout in the State of Washington (Campton and Johnston 1985), and among native subspecies of cutthroat trout (*Oncorhynchus clarki*, formerly *Salmo clarki*) in the western United States (Allendorf and Leary 1988). In some cases, introgressed and native populations coexist in the same regions, and there is considerable concern that some native populations are in imminent danger of loss through introgression or displacement (e.g. Allendorf et al. 1980; Ryman 1981b; Allendorf and Leary 1988; Garcia-Marin et al. 1991).

A reduction of genetic divergence among hatchery populations of chinook salmon in the lower Columbia River, USA, was postulated by Simon (1972) because of high rates of transplantation and straying among hatcheries, and subsequently verified on the basis of similar allele frequencies across several hatchery populations at 25 polymorphic loci (Utter et al. 1989). Such an effect on the population genetic structure has also been observed among wild populations of brown trout in Sweden following massive releases of hatchery-produced fish (Ryman 1981b).

At the opposite extreme are reports of no detectable introgression into indigenous populations despite substantial introductions from exogenous stocks. Presumably, the exogenous fish have been unable to reproduce successfully in the new environments. A notable example of apparent lack of introgression occurs in arid environments in southern Idaho, USA, which support populations of morphologically divergent rainbow trout called "redband" and which have been heavily planted with exogenous cultured rainbow trout (Wishard et al. 1984). Similarly, offspring of anadromous Atlantic salmon released above impassable waterfalls have had no detectable effect on the local nonanadromous populations (Vuorinen and Berg 1989).

Releases of salmonids into areas beyond their natural geographical range appear to be accompanied by increasing hybridization rates with closely related native species. Such hybridization has occurred between released brown trout and native Atlantic salmon in Newfoundland (Verspoor 1988) and between released rainbow trout and native cutthroat trout in the western United States (Allendorf and Leary 1988). One study indicated that interspecific hybridization rates may increase as a result of releases of exogenous stocks of one species even in areas where the two species coexist naturally (Garcia de Leániz and Verspoor 1989).

Genetic Effects on Performance Traits

Although demonstrations of interbreeding between natural and cultured populations have generated considerable conjecture about correlated adaptive changes in natural populations, interbreeding by itself provides no direct evidence for adaptive changes. However, a few experiments addressing the question of adaptive changes have been carried out, and a considerable body of relevant indirect evidence also exists (Table 1).

A direct effect on stock size appears to be reflected in the returns following the previously mentioned translocated chum salmon on Sakhalin Island (Altukhov 1981). Another example relates to an attempt to rebuild coho salmon populations in Oregon, USA, by stocking hatchery presmolts (Nickelson et al. 1986). Although the juvenile density in 15 stocked streams surpassed that in 15 unstocked streams during the summers following stocking, the density of returning adults did not differ between the two groups, and juveniles were less abundant in the stocked than in the unstocked streams in the subsequent generation. This reduction in juvenile density was attributed to earlier spawning of the hatchery coho salmon, which apparently contributed very little to recruitment.

In other instances, a genetic basis for reduced stock size of the recipient population has been identified. The Norwegian Atlantic salmon is presently threatened by the monogenean *Gyrodactylus salaris*, which appears to have been brought to Atlantic drainages via transplanted eggs or juvenile fish from the Baltic (Johnsen and Jensen 1986), where stocks resistant to the parasite have been found (Bakke et al. 1990). Lack of resistance has resulted in the decimation of Atlantic salmon populations in more than 30 Norwegian rivers following fish introductions from hatcheries infected by this parasite.

Indirect effects on stock size may occur where small natural populations are being overharvested in a mixed fishery with more abundant cultured fish (cf. Larkin 1981; Wright 1981). An example of this problem occurred in the management of a fishery of steelhead trout in the Skagit River, USA, which had been based on the assumption that natural reproduction was sustained by both wild and hatchery fish. The finding that gene frequencies of naturally reproduced juvenile fish were typical of those of wild populations of that region rather than of the hatchery population indicated a predominance of wild parents. Consequently, the small run of wild fish had to be protected in order not to reduce the population size of effectively reproducing fish (D. Campton, University of Florida, Gainesville, FL, pers. comm.). All wild fish that are caught (identified by the presence of an adipose fin which is removed from juvenile hatchery fish) are now required to be released in order to reduce the harvest of the wild population.

A similar example concerns a decline that was observed in natural populations of coho salmon in the Yaquina River adjacent to a large sea ranching facility in Oregon. It has been concluded that this decline was caused by environmental changes resulting from the ranching operation. Among other things, it appears that predators were attracted in large numbers to the points of rearing and release of the cultured fish, and these artificially attracted predators also fed excessively on the wild fish (Anonymous 1987b).

Several studies have identified changes of performance traits suggesting that cultured fish were not adapted to the environ-

ment in which they were released. One experimental study with steelhead trout indicated a direct genetic basis for reduced juvenile survival, which was higher in wild fish than in either exogenous cultured fish or in wild × cultured hybrids (Reisenbichler and McIntyre 1977). Different survival of local and exogenous fish during other life stages is suggested by a reciprocal transplantation experiment with masu salmon (*Oncorhynchus masou*) (Mayama et al. 1989), where the local stock outperformed the transplanted one both with respect to the proportion of fish recovered in or near the river of release and the subsequent survival in the river prior to spawning. Other studies showed that genetic changes presumably occur in hatchery-propagated salmonids that reduce their performance in the wild, for example regarding swimming stamina (Green 1964), territorial behavior (Norman 1987), and concealment behavior (Vincent 1960) of juveniles and straying rate of returning adults (Bams 1976). For many of the performance traits studied, hybrids between local and exogenous stocks were intermediate between the parental groups (Bams 1976; Brannon 1982; Hemmingsen et al. 1986), indirectly indicating local adaptations.

Associations relating the reduction in performance to genetic or geographical distance between the donor and recipient populations (or their respective locations) have been suggested by some authors. Altukhov and Salmenkova (1987) hypothesized that the return rate of transplanted chum populations is inversely associated with their genetic distance from the recipient population. Similarly, Reisenbichler (1988) presented strong evidence for local adaptation in coho salmon; he showed a negative association between recapture rate of transplanted fish relative to the local stock on the one hand and the geographic distance the transplanted stock had been transferred from its natal stream on the other (see also Ritter 1975; Hansen et al. 1989).

Summary of Observations

It must be stressed that many of the studies reviewed in this paper were not designed to specifically address questions regarding the effects of released fish on natural populations. For example, most observations relating to effects on the population structure did not result from controlled experiments with well-described populations, but from comparisons between the genetic constitution of populations from stocked and unstocked locations. Further, environmental changes such as watercourse regulation for hydropower development preceded several large-scale releases; therefore, the relative importance of the releases alone may remain conjectural. Also, some of the observations in Table 1 may be explained by nongenetic as well as by genetic changes. For example, differences in behavioral traits such as migration and concealment may be a reflection of learning or environmental factors as well as of genetic factors (Jonsson et al. 1990). However, despite some degree of uncertainty, it appears very likely that an underlying genetic basis contributes to many of the observed differences.

It is noteworthy that wherever there is a detectable effect in comparisons between indigenous and exogenous fish (including hybrids), the performance of the indigenous fish is always better. This one-sidedness of empirical observations in favor of the local population does not represent a conscious bias in selecting references, but appears to point to a lack of observations in the opposite direction. Ricker (1972) similarly concluded that local populations of Pacific salmon were adapted to specific local environments based on a review of numerous studies involving time of return and homing. This overall picture is by no means unexpected. Most local populations should be adapted to their particular environmental conditions, and it is very unlikely that any intentional or unintentional genetic manipulation would result in anything but poorer performance.

Cumulatively, the empirical observations support our concerns about the expectation of a generally negative impact resulting from interactions between cultured and natural populations of salmonids. Specifically:

(1) Recent expansion of marine net-pen rearings has been accompanied by an increased number of accidental escapes. For example, the number of escaped salmon returning to spawn in many rivers now exceeds that of naturally produced fish, and many of these escaped fish are successfully spawning.

(2) The direct genetic consequences when cultured fish come in contact with indigenous populations vary from complete introgression to no detectable effects on genetic population structure.

(3) Even in cases where there is no indication of introgression, indigenous populations may be indirectly threatened genetically by reduced population sizes resulting from increased rates of harvest or predation due to coexistence with large numbers of cultured fish (mixed fisheries).

(4) Although based on limited direct evidence but considerable indirect evidence, it appears clear that local populations of salmonid fishes are adapted to their specific environments. Thus, any substantial influx of exogenous genes, may it be gene flow or complete displacement, has a negative effect on performance. In some instances, severe population reductions have followed introductions of cultured fish.

(5) It follows directly from (2) through (4) that a priori predictions concerning the overall genetic as well as other biological effects cannot be made for any specific instance of interaction between exogenous fish and indigenous populations.

Implications of Gene Flow from Cultured to Indigenous Populations

The difficulty in predicting the effects of influxes of exogenous fishes on local populations is consistent with population genetics theory (e.g. Crow and Kimura 1970). Reliable predictions would require that all of the necessary parameters be known; but this never occurs in real situations. For example, we have virtually no idea of the mode and magnitude of past and present selective forces acting upon those populations or their evolutionary history. Similarly, even basic parameters such as absolute and effective population sizes and migration patterns are poorly known at best. Thus, we have almost no idea of the extent to which most genes are subjected to selection and genetic drift. Further, for most traits, particularly those such as growth rate, disease resistance, etc., that are of direct interest to aquaculture, the genetic basis for their variation remains largely unknown.

It is not surprising, then, to find that the inability to predict the full spectrum of biological effects is increasingly being stressed whenever translocations are seriously discussed (Crawley 1986). For example, the need for empirical risk assessment studies preceding any decision whether or not to release genetically engineered organisms has been noted based on the inability of theory alone to resolve a particular issue (Simonsen and Levin 1988). Furthermore, a need for advanced empirical data preceding releases of any organism into nonnative habitats has been identified, based on numerous examples of ecological disasters resulting from (intentional or

inadvertent) past releases of plants and animals (Mooney and Drake 1989).

The transfer of Atlantic salmon from Baltic drainages to Norwegian waters represents an example that brings the above considerations into focus. The existence of the entire Norwegian population of Atlantic salmon is now threatened by the monogenean *G. salaris*. This parasite appears to have been brought by infected fish from hatchery populations of Baltic origin. Biochemical genetic studies have shown that Baltic and Atlantic populations are genetically distinct (Ryman 1983; Ståhl 1987) to the extent that there is considerable room for adaptive divergence, and recent laboratory tests have found Atlantic salmon from the Baltic to show resistance to *G. salaris* (Bakke et al. 1990). Had this distinctness been known at an earlier time, it should have been recognized as a strong warning against the possible unpredictable consequences of transfer between Baltic and Atlantic populations.

Although the ability of exogenous fish to reproduce successfully in a new environment appears to be difficult to predict, reduced fitness of resultant progeny is expected if the concept of local adaptation is accepted. Successful breedings between individuals from a wild population and those of any exogenous source alter the genetic makeup of the wild population. Presumably, complex genetic interactions to a specific environment that were built up over time are broken down by the hybridization process. A comprehensive discussion of this so-called "outbreeding depression" with examples from various species was given by Templeton (1986). Thus the above observation of generally superior performance of local populations is consistent with the concept of local adaptation.

A contrasting view concerning local adaptation is represented by proponents of the idea that hybrids between specifically adapted cultured fish stocks and wild populations could be used to add new genetic variation to wild populations and thereby increase the potential of the wild populations to adapt to conditions of environmental instability and genetic depletion (Moav et al. 1978; Wohlfarth 1986). Nelson and Soulé (1987) argued against this idea and pointed out that naturally adapted gene complexes of salmonids have been irreversibly compromised by introgressive hybridization with introduced exogenous stocks. They noted that while a very limited degree of introgression may provide a beneficial stimulus to a wild population through providing new alleles without destroying local adaptation (Allendorf 1983), the loss of genotypic variance resulting from massive hybridization of two populations is as irreversible as the loss of alleles from a population. Furthermore, it is not likely that cultured stocks possess advantageous alleles unavailable to a local population through straying from other wild fish populations (Reisenbichler 1984).

As an example of such loss of genetic variance, let us consider hybridization between two populations that are genetically distinct and fixed for different alleles at, say, 10 loci. Such a situation is generally unlikely to be observed among conspecific populations at, for example, protein coding loci, but may well occur at loci determining characters that are more likely to be directly affected by natural selection such as morphological, behavioral, or physiological ones (e.g. Cavalli-Sforza and Bodmer 1971). The resulting hybrid population will contain all the alleles of both populations. However, the original parental genotypes will occur with very low probabilities, less than 1/1000 for each of them. Even a fairly large group of spawners, say several hundred, is not expected to contain a single individual identical to either of the original parental populations. Thus, although all the original genes are present in the hybrid population, the distinctness and individuality of the parent populations are essentially lost. The ultimate outcome of large-scale hybridization is therefore a loss of biological diversity among populations; and the species that was originally characterized by morphologically distinct populations would be replaced by "mongrel" populations that largely lacked the characteristics that existed prior to hybridization (Allendorf and Leary 1988).

Consequences of Complacency

The biological implications of the above combined observations are disturbing. This discomfort is particularly strong in the light of the increasing numbers of fish that are being released either intentionally or unintentionally coupled with the decreasing number of natural populations that remain largely unaffected by other effects of human activity. What actions, then, can be taken in view of this knowledge and these concerns?

Let us first consider doing nothing as an appropriate response. Certainly, arguments could be raised in justification of this approach. For example, a high likelihood of no effect between (in particular) escaped pen-reared fish and natural populations might be argued. Most pen-reared populations have genetically adapted to conditions of culture (Gjedrem et al. 1988) and would possibly not spawn successfully, should they migrate to spawning areas. Unfortunately, these arguments fail to stand up to the observations of significant migrations to and successful spawnings in rivers inhabited by native populations.

A proponent of "doing nothing" could still claim that escaped fish that successfully reproduce — either amongst themselves or through hybridization with indigenous fish — are in fact genetically enhancing the populations where they breed. "Doesn't successful reproduction reflect survival of the fittest? And isn't hybridization an effective means of improving performance?" However, there are clear responses to these arguments. Successful spawning of exogenous fish to the point of replacing an indigenous population would tell nothing about the relative fitnesses of the two groups in the absence of additional data. For example, the exogenous fish may overcrowd the spawning environment sufficiently to displace the native stock, but the consequent alien juveniles may fail dismally through the remainder of the life cycle. The occurrence of such failure is strongly supported by the cumulative impact of the studies summarized in Table 1. Furthermore, those progeny of alien fish that might return would lack the opportunity to possibly establish a readapted population if the flooding of alien parents persisted.

Nevertheless, the "do nothing" approach may still be invoked by questioning the actual value of natural populations, given the abundance of cultured fish and the fact that escaped fish are substantially contributing to commercial and sport fisheries in some areas. In response to such an argument, it is useful to extrapolate from present trends to speculate, as a hypothetical example, about conditions that present trends suggest might typify the situation for Atlantic salmon in Norway in the year 2000: a fishery is being maintained — particularly in proximity of net-pen culture — by escapes from a thriving net-pen industry; natural populations have been largely eliminated as a combined result of *G. salaris* infestations and their inability to compete with continuing and abundant influxes of escaped salmon whose progeny do not return in substantial numbers; an epidemic suddenly sweeps through the net-pen industry resulting

in a crash of both the industry and the incidental fishery that it supports; in this situation, recovery is unlikely because of the absence of resistant populations to provide seed for new aquacultural stocks.

This scenario is much more than mere fantasy. The motivation behind such legislation as the *United States Endangered Species Act of 1973* goes beyond the aesthetic and cultural values in protecting threatened or endangered distinct populations within a species (cf. Utter 1981; Meffe 1987); the evolutionary future of the species — including its aquacultural value — lies in such preservation. Loss of distinct genes as well as the above-mentioned gene combinations that are preserved in natural populations destroys a necessary reservoir of genetic variation. Without this reservoir, the species becomes highly vulnerable to environmental changes or to epidemics from which it may be incapable of recovering.

Strategies for Minimizing Genetic Impact on Natural Populations

The need for aquaculture of both intentionally released and captive populations will persist, but the empirical evidence presented here shows that such activities frequently compromise natural genetic resources. Therefore, measures to minimize this negative impact are strongly needed. A number of such measures are discussed below.

Closed Culture

The most obvious way to reduce gene flow from a closed environment is to keep the number of escaped fish at a minimum. It may be argued that this number is already minimal as a consequence of the economics of fish farming; it is pointless to raise fish that escape. However, it is evident in many places (e.g. Norway) that too many fish presently escape from the perspective of maintaining the integrity of the wild populations. Therefore, measures imposed through legislation appear to be required to achieve adequate reductions of current escape rates.

Marine-based operations may move inland, where containment can be much more readily achieved. In fact, a formerly marine-based coho salmon rearing operation in the northwest United States has recently moved inland and has become exclusively land based. This operation (Domsea Farms, Pocatello, Idaho) was formerly a marine net-pen facility. The move was economically motivated because of disease, predator, and maintenance problems at the original marine location (E. Brauer, Domsea Farms, pers. comm.). This relocation serves as a viable model for other operations.

Sterilization

Sterilization is an option for reducing gene flow that can be applied either in closed culture or sea ranching operations. Sterility can be induced without difficulty in salmonids either through hormonal treatments of juvenile fish (Solar et al. 1984) or by induction of triploidy shortly after fertilization (Chourrout 1987). For some species (e.g. rainbow trout in Great Britain) the production of sterile fish has reached a high level (Bye and Lincoln 1986). However, there are presently unresolved concerns that must be considered if sterilized fish are used. Escaped or intentionally released sterile fish still have the potential to spread pathogens. Also, little is known about the behavior of sterilized salmonids. What little is known relates to studies of hormonally sterilized coho salmon released near Vancouver, British Columbia, Canada, in the Strait of Georgia (Solar et al. 1986). Sterilized females and some males remained in the fishery for at least 2 yr beyond their normal life span. However, some of the hormonally treated males returned to the point of release concurrent with control fish of both sexes. These treated males had developed both secondary sexual characteristics and fragments of gonadal tissue (E. M. Donaldson, Department of Fisheries and Oceans, pers. comm.). Similar sexual development is a common occurrence among triploidized male salmonids (Bye and Lincoln 1986). The possibility of sterile but sexually active male salmonids competing in courtship with fertile males brings to mind the successful eradication of mosquito populations intentionally flooded with sterile but sexually active males (Patterson et al. 1970). This problem possibly could be averted through mandatory use of all female populations (Bye and Lincoln 1986), but even here it is unsettling to consider a marine environment populated with perpetually immature and continually growing female salmonids. Much more empirical data are required before large-scale releases of sterilized salmonids can be considered as a responsible option for aquaculture.

Localization

Gene flow from cultured to wild populations can also be reduced through confining the locations of both the culture operations and — in instances where fish are to be intentionally released — the point of release. For example, it has been observed for Atlantic salmon that the proportion of pen-reared fish in rivers decreases with increasing distance between the river and the nearest fish farm; up to 80% of the spawners were of pen-reared origin in rivers within areas of intense fish culture, and this proportion dropped dramatically as distance increased (Gausen and Moen 1991). Although rivers far away from net-pen operations are not entirely protected from escapees, they receive fewer of them than rivers closer to the fish farms and will therefore probably be genetically affected at a slower rate.

Fish that return to a marine release site will eventually ascend rivers in the neighborhood for spawning. Therefore, it is imperative that such fish are captured with high efficiency while still at sea. The development of a fishery that selectively captures released fish at sea is strongly needed and may perhaps be aided by applying recently acquired knowledge of differences in spatial and temporal migration patterns between wild and experimentally released fish (Hansen et al. 1987, 1989; Gunnerød et al. 1988; Jonsson et al. 1990).

Sea ranching operations should preferentially release smolts in large rivers or in bays or estuaries having a single major drainage because straying to other rivers appears to be reduced under such conditions (Quinn and Fresh 1984). Large rivers that have lost their original salmonid populations due to pollution or hydropower development would be excellent candidates for large-scale sea ranching. Another option is to limit sea ranching operations to restricted areas. Such a policy is currently used by the Washington State Department of Fisheries, which has set aside 25% of Puget Sound for management based on release and capture of hatchery produced coho salmon, while the remainder of Puget Sound is managed exclusively on the basis of natural reproduction (Wright 1981). Such a policy acknowledges the importance of wild populations, particularly

in areas where fisheries are dependent both on existing hatcheries and naturally reproducing populations.

The idea of totally protected areas such as national parks represents an extension of the above action of setting aside areas for management totally based on natural reproduction. Such a measure is probably needed in countries such as Norway where escape rates are increasing dramatically and no populations except those located sufficiently distant from aquacultural operations are likely to remain reasonably uncontaminated (Ståhl and Hindar 1988). We strongly urge such actions before there is nothing left to protect.

Minimal Genetic Differences from Indigenous Populations

The effects of gene flow can be reduced by assuring that the genetic differences between escaping or released fish and the recipient wild populations are as small as possible. One way to achieve this objective of minimal differences is to strive for aquaculture programs that are based on local populations as much as possible. This process will not prevent the cultured stocks from becoming increasingly different from their wild ancestors because of selective breeding within the aquaculture program and the inevitable process of domestication. It will, however, prevent the introduction of highly exotic genes (and pathogens) into local wild populations.

Monitoring the Genetic Effects of Aquaculture

Genetic differences between cultured and natural populations (e.g. at protein coding loci) must be identified and quantified prior to any release if effective monitoring of gene flow is to occur. It is therefore important that adequate amounts of this kind of genetic information be available both for cultured populations and for wild populations that may be affected by migration from them.

Fish culture stocks have generally not been established with the intention of creating detectable genetic differences from wild populations. However, such differences can be straightforwardly induced without altering the performance of the cultured stock (Parker et al. 1990) provided that appropriate recommendations (e.g. for minimizing inbreeding) are followed. Such "genetic marking" should generally be a requirement for cultured stocks that are not otherwise genetically identifiable. The only exception to this requirement would be short-term culture operations aimed at supplementing a native population and using only spawners from that population (cf. Allendorf and Ryman 1987). We consider this requirement to be the most important step to be taken in order to obtain even the vaguest idea of the genetic effects of release of cultured fish on wild populations. Without such a step, these effects will always remain conjectural, and it will not be possible to produce anything but speculations that are based on no empirical evidence.

A second kind of information that appears to be potentially useful in programs for monitoring genetic changes in populations is from morphological variation measured by fluctuating asymmetry of bilateral characters (e.g. Leary et al. 1985). Increase in levels of asymmetry have been shown to be sensitive indications of loss of genetic variation (Leary and Allendorf 1989). The monitoring applications of this kind of data were summarized by Allendorf and Ryman (1987); they pointed out the complementary nature of asymmetry measurements to biochemical genetic information, particularly with regard to early detection of morphological effects due to loss of genetic variability in a population. As with biochemical genetic studies, adequate sets of baseline data must be available from potentially affected wild populations for subsequent changes in asymmetry to be measured.

A systematic monitoring of wild populations for gene flow from intentional or unintentional releases of cultured fish can proceed once adequate genetic distinction exists between cultured and wild populations. This monitoring process permits a posteriori actions following the detection of successful breeding of cultured fish. Details concerning the appropriate actions to be taken following the detection of gene flow to wild populations lie beyond the scope of this paper. The detection of a substantial genetic intrusion into wild populations is a serious matter that requires immediate adjustments of aquacultural practices. Also, it must be stressed that monitoring must not be used as an excuse for doing nothing about the aquaculture operation creating the unwanted effects any more than merely appointing a committee can be considered the solution to any problem.

Recommendations

The International Symposium of Fish Gene Pools, Preservation of Genetic Resources in Relation to Wild Fish Stocks, was held in Stockholm in January of 1980. The participants of this meeting formulated a set of recommendations to serve as guidelines for the management of genetic resources in natural populations (Ryman 1981a). These recommendations are summarized in the following action statements:

- Identify genetic resources.
- Maintain natural ecosystems.
- Maintain genetic variability.
- Avoid selective harvest of natural populations.
- Preserve genetic variability within cultured populations.
- Release fish into natural environment with great care.
- Provide adequate funding for basic and applied research.
- Inform those responsible for management of existing knowledge.

Nothing has changed during the intervening decade to reduce the vitality and currency of these recommendations. Indeed, the only change is that the urgency for their implementation has increased because of aquacultural growth, continued habitat degradations, and — unfortunately — continued losses of genetic resources due to failure to adequately carry out these recommendations. We stress that the primary issue of the present paper is *not* to point to the need for more research. Rather we stress the need for immediate action based on everything that is already known. We therefore affirm these existing recommendations from the Fish Gene Pools Symposium as the underlying basis for the ones stated below that are more specifically related to the genetic effects of aquaculture on natural fish populations.

(1) All aquacultural activities should be conducted in a manner that minimizes potential gene flow to wild populations.

(2) Aquacultural facilities should be located and designed to minimize the possibility of escaping.

(3) Locations for aquacultural rearing and release should be selected on the basis of having minimal impact upon natural populations; whenever needed, areas for complete protection should be set aside and located to assure minimum impact from aquaculture operations.

(4) Movements among areas should be restricted to guard against the importation of individuals that may carry pathogens to which local forms lack resistance.

(5) A cataloguing of genetic characteristics of natural populations that would potentially be genetically affected by aquacultural releases (e.g. allele frequencies, spawning times, life history variables, etc.) should accompany any aquacultural activity to serve as baseline data for subsequent monitoring.

(6) Cultured populations subject to potential escape or to release should have heritable characteristics (i.e. genetic marks) that permit monitoring introgression with natural populations or establishment of self-sustaining populations.

(7) A variety of experiments designed to provide empirical data concerning the genetic effects of aquacultural activities on natural populations should be carried out. Particularly important are experimental releases of genetically identifiable fish, which should precede any proposed large-scale rearing or release, and the results of which should dictate the scope of such activities.

(8) Rearing of sterile fish for aquaculture should be encouraged through use of sterile hybrids and applications of such procedures as induced triploidy and hormonal sterilization. However, an understanding of the potential ecological and genetic effects of releasing such individuals should precede any large-scale rearing or release.

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ANNOUNCEMENTS/AVIS

Canadian Conference for Fisheries Research (CCFFR)

Dalhousie University
Halifax, Nova Scotia
January 3–4, 1992

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This conference will be held in Halifax, N.S., January 3 and 4, 1992. The major themes of the conference will be (1) Large-Scale Environmental Effects on Fish Survival and Abundance, (2) Role of the Early Life History Stage in Population Dynamics, and (3) Migration, Mixing and Dispersal in Fish and Invertebrate Stocks.

While papers on other themes may be submitted, authors are encouraged to adhere to the above themes as much as possible.

Deadline for abstracts is August 30, 1991. They should be typed (maximum 200 words, single spaced) and nature of presentation (oral/poster) indicated. A high quality of copy is required, suitable for photographic reproduction.

Abstracts should be addressed to Dr. Steve Campana, Bedford Institute of Oceanography, Biological Sciences Branch, Department of Fisheries and Oceans, P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada. Telephone: (902) 426-3233.

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Université Dalhousie
Halifax, Nouvelle-Écosse
les 3 et 4 janvier 1992

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